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WOODPECKERS (PICIDAE)

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NOTES ON WOODPECKERS (PICIDAE)

BY

D. GOODWIN

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TRUSTEES OF
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NOTES ON WOODPECKERS (PICIDAE)

By D. GOODWIN

THESE notes are based on examination of the woodpeckers, Picidae, in the British Museum (Natural History) during revision and re-arrangement of the collection. The only species I know in life are the Green Woodpecker *Picus viridis*, the Greater Spotted Woodpecker *Dendrocopos major* and the Lesser Spotted Woodpecker *D. minor*; I have also briefly observed the Grey-headed Woodpecker *Picus canus*, the Black Woodpecker *Dryocopus martius*, the Syrian Woodpecker *Dendrocopos syriacus*, the Middle Spotted Woodpecker *D. medius*, the Hairy Woodpecker *D. villosus*, the Downy Woodpecker *D. pubescens*, the Sapsucker *Sphyrapicus varius*, the Red-bellied Woodpecker *Melanerpes carolinus* and the Golden-shafted Flicker *Colaptes auratus* during visits to Austria and North America.

Suggestions or conclusions presented here are, therefore, based mainly on external morphological characters. For this reason I have not suggested alterations from the most recent comprehensive check list (Peters, 1948) except when the evidence in favour of such a course appears overwhelming.

Section 1: General notes on the family

REMARKS ON AFFINITIES, CONVERGENCE AND COLORATION

Peters (1948) divides the true woodpeckers (Picinae) into two major groups on the basis of correlated foot and bill characters: those in which the outer hind toe is not longer than the outer front toe, the nasal shelf narrower and the nostril near the culmen; and those which have the outer hind toe longer than the outer front toe, a wider nasal shelf, and the nostril mid-way between the culmen and the edge of the upper mandible or nearer the latter. When the woodpeckers are thus divided into two groups two significant correlations emerge. First, most, if not all, genera, many or all of whose members are known to be partly or entirely ground feeders, or to feed largely by picking insects from the surface of trunks, branches or leaves or by fly-catching, come into the first group. This is the case with *Nesoceleus*, *Picus*, *Dryocopus*, *Melanerpes*, *Asyndesmus, and Micropternus*. Second, some " pairs " of genera whose geographical distributions, colour patterns and general similarity suggest close relationships between them—*Geocolaptes* and *Mesopicos*, *Micropternus* and *Blythipicus*, and *Dinopium* and *Chrysocolaptes*—are separated. Thus it seems likely that these bill and foot differences may be rather labile adaptive characters and that the toe formation may have become differentiated in closely related forms in the course of adaptive radiation.

In Europe woodpeckers divide easily into four taxonomically distinct genera—*Picus*, *Dryocopus*, *Dendrocopus* and *Picoïdes*—with no troublesome intermediate forms. The same does not hold true for most other geographical regions. Even such visually striking differences in coloration as those between " pied " woodpeckers and " green " woodpeckers are bridged by " pied " woodpeckers that show considerable yellow or green suffusion, such as *Dendrocopos temminckii* and *Melanerpes* *striatus*; and by " green woodpeckers, such as *Veniliornis spilogaster*, which, show an underlying pattern virtually identical to that of some of the black and white forms. As in other groups of birds there is evidence that relatively concolorous forms with a simplified colour pattern can derive from forms with a more complex pattern, although in the woodpeckers most of these are still at a stage where their affinities are obvious; for example *Melanerpes herminieri* and *Sapheopipo noguchii*.

The following general trends in coloration and colour pattern are evident. Forest forms tend to have boldly patterned black and white colour patterns, usually with red or yellow signal or display markings. Forms inhabiting more open woodland are usually more cryptic; either through a predominantly olive-green colour, at least on the upper parts; or, when predominantly black and white in coloration, through a barred (" ladder-backed ") or profusely mottled pattern. Forms that have become largely terrestial tend to be more fully cryptically coloured, and show reduction or absence of the red or yellow markings on crown or nape that are otherwise so nearly universal in the woodpeckers. In view of the number of species whose behaviour and ecology are little known the above remarks are, of course, tentative. On the other hand, apparent exceptions to those general rules may prove not to be so when we have further information. For example, the Syrian Woodpecker *D. syriacus* which is black and white with a red nuchal patch in the male inhabits, at least in its European range, rather open cultivated and settled regions, but this choice of open habitat may be, in an evolutionary sense, a recent development. Again, the Green Woodpecker *P. viridis* feeds largely on the ground through it appears colourful enough at close quarters. When, however, it is on the ground in typical feeding sites, such as grassy slopes, parkland, and woodland openings, its plumage is highly procryptic and even the red on its head, which is darker and less " fiery " in tone than that of many more arboreal species, does not show up very conspicuously. It must be mentioned that conspicuous red, yellow or white rumps can be concealed by the folded wings, and they usually are when their owners are alarmed, so that their possession by such species as the Ground Woodpecker *Geocolaptes olivaceus* and the Andean Flicker *Colaptes rupicola*, does not significantly affect the cryptic character of the rest of their plumage.

There are widely separated allopatric forms that show considerable general resemblance to each other. In some cases the details of their respective colour patterns make it fairly certain that the resemblance is due to convergence. This is so, for example, with the two ground-living woodpeckers, *Colaptes rupicola* of South America and *Geocolaptes olivaceus* of South Africa, whose affinities are clearly with other American and African forms respectively, not with each other. The Chestnut-coloured Woodpecker *Celeus castaneus* of Central America is related most closely to other *Celeus* species, and thence to other American genera, and is, obviously, not at all closely allied to the Asiatic Rufous Woodpecker *Micropternus brachyurus*, to which its rufous, black-barred plumage gives it considerable superficial resemblance. The small green woodpeckers of Central and South America, of the genus *Veniliornis*, show such close resemblance to the African genera *Dendropicos and Campethera* that I feel uncertain whether this is due to genuine close affinity or to convergence, although I think the former less likely.

The Ethiopian region has no arboreal woodpecker that is very large in size. Although the smallest woodpeckers in the Nearctic, Neotropical and Oriental regions are all about the same size, the largest arboreal African woodpeckers (*Thripias*) are much smaller than the largest arboreal species in all the other woodpecker-inhabited regions. The largest African species, the terrestial *Geocolaptes olivaceus*, is, however, about the same size as, or only a little smaller than species that are equally (*Colaptes rupicola*) or to some considerable extent (other *Colaptes* species, some *Picus* species) terrestial in the Nearctic, Palearctic and Neotropical regions. Also no African woodpecker is boldly black and white in colour although the African barbets have produced some predominantly black and white species.

Another interesting fact is that although all other continents inhabited by woodpeckers have several very similarly coloured " green " woodpeckers, there are no green species in North America, where their ecological equivalents would seem to be the brownish and barred flickers, *Colaptes*, and the " ladder-backed " species of *Melanerpes* (*Centurus*).

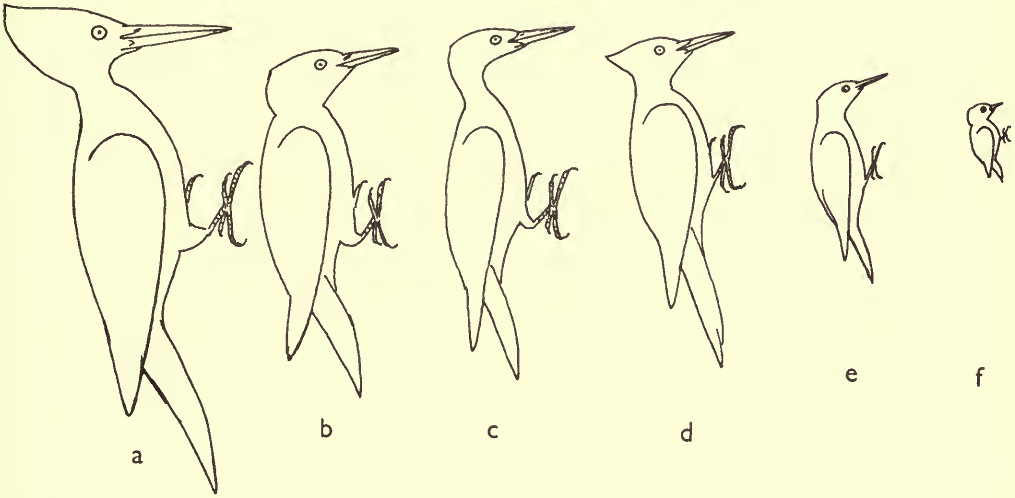

FIG. 1. (a to e) Diagrammatic outline sketches of the largest species of arboreal woodpecker in, respectively, the Nearctic, Palearctic, Oriental, Neotropical and Ethiopian regions; f shows comparative size of the smallest woodpecker species (piculets excluded) in all of the above regions. It should be noted that the largest Nearctic species, the Imperial Woodpecker *Campephilus imperialis*, is rare and restricted in range; the largest widespread species in the Nearctic, the Pileated Woodpecker, *Phloeoceastes pileatus*, is approximately the same size as the largest species in each other region, the Ethiopian excepted.

SEXUAL DIMORPHISM

The great majority of woodpeckers are sexually dichromatic. In nearly all the difference consists of the male having red or, less often, yellow areas on the head that are absent in the female. This may involve only the male having red on the head or both sexes may have heads that are predominantly red in colour but still with the female having a little less than the male. Even in species such as *Colaptes rupicola* and *Micropternus brachyurus*, in which the male has only a little rather dull red on the malar region, the sexual distinction is clear cut and not just a matter of the male being slightly brighter or having his bright colours slightly more extensive than the female's. This latter form of sexual dichromatism, common in so many birds, is found in only a very few woodpeckers.

Only in five species are the sexes alike or nearly so. These are the Middle-spotted Woodpecker *Dendrocopos medius*, the Sapsucker *Sphyrapicus varius* (the predominantly red-headed races *daggetti* and *nuchalis*) Lewis's Woodpecker *Asyndesmus lewis*, the Red-headed Woodpecker, *Melanerpes erythrocephalus* and the Porto Rican Woodpecker *M. portoricensis*. In *D. medius*, both sexes have the crown red, a very common feature of males of allied *Dendrocopos* species. There is, however, some sexual difference in that the red on the female is not quite so bright as on the male and does not usually reach quite so far back on the nape where it is tinged with yellow. This is the kind of sexual dimorphism common to most bird species in which the sexes are usually said to be alike. It would, presumably, not give so immediate or positive a clue to sex as the type of difference usual in woodpeckers. In the red-headed form of *S. varius* there is also a marginal tendency for the male to be more intensely coloured, but in *M. erythrocephalus* there is no constant difference in brilliance between the sexes. There does not seem any obvious or likely reason why any of these three forms should be able to dispense with the usual type of sexual dimorphism which, since it is nearly universal, must have, in most species, strong selective value. *D. medius* is, however, sympatric with congeneric and rather similar species, and in its case selection for specific distinctness may have operated at the expense of sexual differentiation. One species that is in many places sympatric with it, *D. leucotos*, is extremely similar in coloration and colour pattern except that the female has a black instead of a red crown; it is also larger in size.

Asyndesmus lewis is a rather aberrant species which differs much in feeding habits from the more typical woodpeckers (see Bent, 1939). Its colour pattern, although showing some connections with those of some *Melanerpes* species, to which it is clearly allied, is unusual and it has no red on crown or nape. Typically the female is marginally duller than the male. *M. portoricensis* shows in extreme degree the loss of distinctive markings common in isolated island forms, being all black except for a dark reddish tinge on the underparts. The sexes are alike.

Colaptes auratus is the only species which shows both conspicuous red markings (a red nuchal band) and clear cut sexual dimorphism that does not involve a lack of red in the female, the male alone having black malar stripes. Other flickers, leaving aside for the moment the aberrant Fernandina's Flicker *Nesoceleus*, differ sexually in the male having red or partially red malar stripes and the female not. In *C. pitius* the red on the malar stripes of the male is reduced to a pale, dull pink on the tips of the feathers, whose bases are blackish, so that the sexual difference in this species is somewhat intermediate in character between that of *auratus* and other flickers although less conspicuous than in either.

The only woodpeckers in which neither sex shows a trace of red or yellow in the plumage are *Nesoceleus fernandinus* and the Heart-spotted Woodpecker *Hemicircus* *canente*. In *Nesoceleus* the sexes differ in the male having a black and the female a speckled malar stripe; in *H. canente* the male has the forehead and crown white, the female has a spotted forehead and crown.

Besides the colour differences described above female woodpeckers, like the females of most other birds, often average slightly smaller in bill size than the males. In some island forms this difference and the correlated difference in body size is considerable. In a recent important paper on this subject (Selander, 1966) it has been shown that such differences are correlated with sexual differences in feeding ecology and serve to lessen or prevent feeding competition between male and female.

The piculets, sub-family Picumninae, show " typical " woodpecker sexual dimorphism except that in two species the " male's " colour is chestnut, not pure red or yellow.

JUVENILE PLUMAGES

Juvenile woodpeckers, like juvenile barbets, Capitonidae, but unlike most other birds, usually show similar bright red or yellow pigments to those of the adults. In some species, of which the Greater Spotted Woodpecker *Dendrocopos major* is an example, the juvenile male may have differently placed and more extensive red markings than his father, and the juvenile female show red areas that are lacking in the adult female.

Many juvenile woodpeckers have a greater number of attenuated tail feathers similar in character to the stiff, central feathers used to prop the bird when resting or working on a tree trunk than have the adults. The juvenile's wing may show a reduction in size of the two innermost primaries and consequently rather more pointed wing. These facts prompted Kipp (1956) to suggest that the juvenile plumages of woodpeckers represented a probable future stage in their evolution as they could, he thought, neither represent a recapitulation of a prior evolutionary stage nor be of value to the juvenile as distinct from the adult. Verheyen (1957) disagreed with this conclusion; pointing out that, in many other birds, the juvenile rectrices are to some degree narrower and more pointed than the adult's and that the reduction in size of the inner primaries was probably connected with the need for quick growth to enable the early onset of the first moult. This was also discussed by Sibley (1957), who pointed out that this reduction of the innermost primaries occurs in some species only, and is almost certainly adaptive. The Stresemanns (1966) in their comprehensive study on moult in birds agree with this conclusion.

Verheyen also emphasized, correctly, that the juvenile plumage of woodpeckers is, like that of most other birds, usually of a weaker and more downy character than the adult plumage. He suggests that this might be of particular disadvantage to a woodpecker and hence one reason for the quick onset of the first moult. This, in some species, begins before fledging, at which time the two reduced inner primaries above mentioned, may have been replaced by adult feathers. Verheyen suggested that the bright red or yellow pigments of juvenile woodpeckers, and the fact that in many woodpeckers the juveniles show the same sexual dimorphism as the adults, might be due to an original (presumably duller and less dimorphic) juvenile plumage having been completely suppressed in the course of evolution. He considered that the present juvenile plumage was originally the first post-juvenal dress. I think this is an unlikely hypothesis. Except for the bright red or yellow pigments often present, this plumage has the typical characteristics commonly found in juvenile plumages in other groups: a looser and more downy or woolly texture of the contour feathers; weaker shafts of the quill feathers; a tendency for transverse barring, dark or light shaft streaks or pale feather tips (not present or not so pronounced in adult) to be present or more prominent and to give a more spotted or barred general appearance and a tendency for black areas to be browner and less glossy. *All* these characters are not, of course, usually found in the juvenile plumage of any one species.

The red or yellow pigments themselves may be less fully developed in the juvenile plumage. The red is often lighter or more orange-red than that of the adult; and in many species the red tips of the feathers are less extensive, so that the juvenile appears to have a scattering of red speckles where the adult, if in unworn plumage, appears uniform red. In a few cases the lighter red of the juvenile may make it appear more brilliant. Similarly, in those species which have golden yellow instead of red on the head, this is often of a darker and more orange tint in the juvenile. It is possible, however, that in both these instances the juveniles may not appear more impressive to avian as they do to human eyes.

Verheyen divided the African and Eurasian species he studied into four groups: those in which the juveniles resembled the respective adults in their degree of sexual dimorphism; those in which the juveniles resembled neither parent; those in which both sexes resembled the adult male, and those in which both sexes resembled the adult female. Most other woodpeckers fall into one or other of Verheyen's categories, which do not, however, cover the whole range of juvenile plumages. It seems worthwhile to describe briefly the likenesses and differences (*vis à vis* the adult) found in the coloration and sexual dimorphism of the juvenile plumages, and their generic distribution. In so-doing I shall not take account of such minor differences as are generally characteristic of juvenile plumage. Thus a juvenile may be said to be " like the adult " if it has the same colour pattern and general coloration, even though it may, for example, have an orange-red instead of a scarlet cap.

It seems pertinent to digress here to mention the hazards when ascertaining the juvenile plumage in species of which few reliably sexed juvenile specimens are available. It has become very evident in the course of this study, that in the past many collectors have labelled young woodpeckers as males or females according to whether their head coloration most resembled that of the male or female adult. With well-known European and American species this guess-sexing is immediately obvious, but is is much less easy to detect with species represented only by one or two specimens. Another hazard is that in some species, of which the Three-toed Woodpecker, *Picoïdes tridactylus* is an example, the feathers of the forehead and forecrown (sexually differentiated in the adult) are moulted very soon indeed after fledging, so that specimens in almost complete juvenile plumage, but with adult plumage on front and top of the head, may be much commoner in collections than birds in complete juvenile plumage.

In general colour pattern and the (usually sexually dimorphic) head markings, juvenile plumages, come into one or more of the following categories. Categories 2 to 6 involve coloration of male juveniles, 7 to 9 of females, and 10 to 12 of both sexes.

(1) *The juvenile male and female are like respective adults in the extent of red or yellow on the head.*

In this category are some species of *Colaptes*, some (possibly all) species of *Piculus* and *Chrysoptilus*, some species of *Melanerpes* (*cruentatus, formicivorus, candidus* and possibly some others), *Trichopicus* (although in this species the yellow on the throat, which is not a sexual character, is absent in the juvenile), *Celeus flavescens* (most probably other species of *Celeus* also), some species of *Phloeoceastes* (*lineatus, pileatus* and, probably, *schulzi* and *galeatus*), *Dryocopus*, *Picus* (with two possible exceptions and a tendency for restriction of lipochrome pigment in the juveniles of the yellow-naped species), *Gecinulus* (females of both species and males of one), *Dinopium benghalense* and *D. javanense* (but in the latter the front of juvenile's forehead is brownish so that it is intermediate in this character between *benghalense* and the other *Dinopium* species), *Chrysocolaptes* (*festivus* only; although the male of *validus* is very similar to the adult but has yellowish brown throat and malar region), *Dendrocopos* (males of all the red-crowned species and females of a very few species), *Meiglyptes* (but juvenile males often show a reddish tinge on forehead, which is rarer in adult males), *Blythipicus* (*pyrrhotis*), *Micropternus* (but a few juveniles show a trace of red on the nape).

(2) *The juvenile male has less extensive red or yellow areas on head than has the adult male.*

This broad category is best subdivided into the following groups.

(a) *Juvenile male has red (or yellow) only on the hind crown and/or nuchal region, adult male has entire top of head, and sometimes forehead also, red or yellow.* In this group belong the *Campethera* species. In *nubica, punctuligera* and *bennettii* juveniles resemble the adult female in having red only on the hind crown and nape, the forehead and forecrown is, however, more or less dull grey or blackish, not spotted or streaked with white as in adult female. In *maculosa* and *permista* the differences between adult and juvenile males are similar. Our few specimens of juvenile females of these species show less extensive red on the nuchal region than males. In *caroli* and *nivosa*, in which the adult females has no red and the adult male has red only on the nuchal region, the juvenile males appear to have no red and thus resemble the female. This statement is, however, based on only one juvenile male specimen of each species in our collection (which I have reason to believe were reliably sexed) and on Verheyen's description of *caroli*. In *Dinopium rafflesii* the juvenile male has the forehead brownish, shading to blackish on the crown with a few red flecks, narrow greenish gold fringes to some of the feathers and only the hind crown and long nuchal crest red; in *D. shorii* the juvenile male has the forehead streaked dark brown and dull cream; in both these species the adult males have the top of the head entirely red.

In *Chrysocolaptes lucidus* (*guttacristatus* and allied mainland races) the young male also lacks red on the forehead. This species shows, however, an interesting situation. The juvenile male at first has a brownish black forehead, unspotted or with only obscure spots. Before the juvenile plumage as a whole is shed some of the forehead feathers are replaced by boldly spotted ones similar to those on the head of the adult female. These spotted feathers may extend well onto the crown where they have, presumably, replaced juvenile red feathers. Later these spotted feathers are replaced by red ones but some birds show feathers intermediate between the adult red feathers and the black and white spotted feathers, that is red feathers somewhat intermediate in form and with a white spot. These spotted feathers on the forehead do not seem to represent an intermediate plumage in any true sense but they do give the owner's head some " female " characteristics. From the available specimens it is difficult to judge whether differences are due to age or individual variation and observations on living birds are needed.

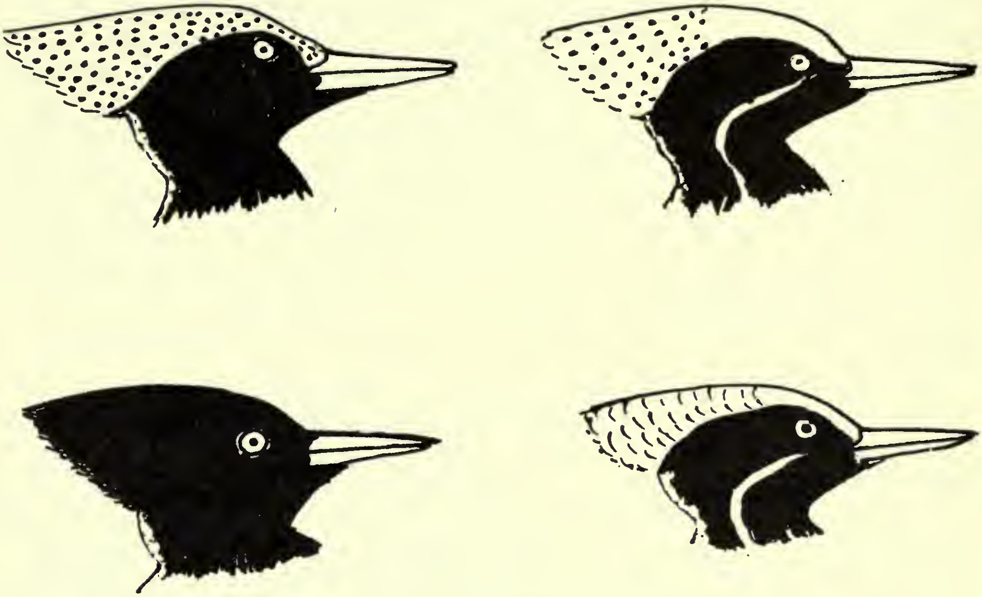

FIG. 2. Diagrammatic sketches of heads of *Hemicircus concretus* to show differences in colour pattern between adults (left) and juveniles (right) of both sexes; males above, females below. Shaded areas are dark grey, stippled areas bright red or orange-red, unshaded areas buff; the scale-like markings on the crest of the juvenile female represent grey feather edges.

Hemicircus concretus shows a striking difference between the juvenile and adult male. The latter has the entire top of the head, from forehead to nuchal crest, bright red, the rest of its head is dark grey. The juvenile male has the forehead and crown buff and only the nuchal crest (ends of the long head feathers) red. In the race *sordidus* the adult has the nuchal area largely grey and the juvenile male has much less red than in the juvenile of the nominate form. In both the juvenile shows a suggestion of a buff malar stripe which is lacking in the adult. It may be mentioned here that although the adult female's head and crest are grey the juvenile female is like the juvenile male except that her nuchal region is buff like her crown, not red.

(b) *Red on juvenile male does not extend to, or so far down, nape as in adult male.* In this group belong only the species of *Mesopicos*.

(c) *Adult male has head largely or entirely red; juvenile male has less red on head.* *Phloeoceastes*: in *guatemalensis* and *melanoleucos*, juveniles are like the adult female, thus having black forehead and forecrown and much less extensive red areas that adult males. In *robustus* (but this is surmised from only one specimen) the juveniles also, probably, resemble the adult female. In *haematogaster*, however, in which, as in *robustus*, the adult female has the forecrown red, the juveniles of both sexes have the forehead and forecrown blackish. They also have buff instead of red rumps although both on rump and head the juvenile feathers are soon replaced. In *leucopogon* the juveniles of both sexes are said (Laubmann, 1930) to have entirely black heads but this statement was based on one moulting juvenile. In *pollens*, the only form in which the female has no red on the head, an unsexed fledgling is like the adult female.

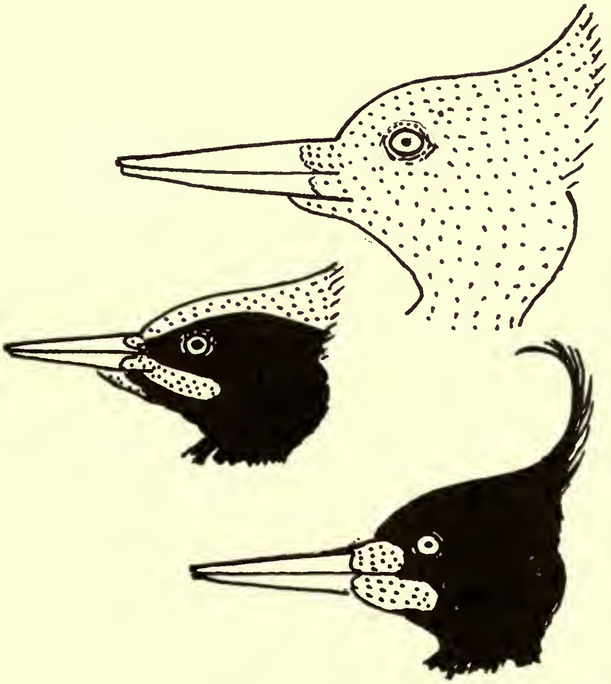

Fig. 3. Diagrammatic sketches to show difference in colour patterns of heads of adults (right) and juvenile male (left centre) of *Ipocrantor magellanicus;* the distribution of red and black on juvenile female is similar to adult female's.

In *Ipocrantor* (*magellanicus*) the male has the head entirely red; the juvenile male has a black head with forehead, crown, nape, malar stripes and chin red. Both juvenile and adult females have only the chin and loral region red.

In the red-headed forms of *Sphyrapicus varius* (*ruber* and *daggetti*) the generally smoky-brown juvenile has the head extensively tinged with red but this red is not so extensive and not nearly so bright as that of the adult. So far as adult-juvenile differences are concerned the situation is the same with those races of *varius* in which the adults have less red on the head.

(d) *Adult male has some red on head, juvenile male has none.*

In *Campethera nivosa* and *C. caroli* the adult males (but not the females) have red on the nape, although in *carola* this is reduced to a scattering of red-tipped feathers. If a male and a female juvenile of *carola* and a male juvenile of *nivosa* are correctly sexed, as I believe to be the case, then in neither of these species has the juvenile male any red on the head. The juvenile of *caroli* (both sexes) also differs in having less yellow pigment, in the top of its head being blackish brown instead of dark green and the yellow, dark-speckled throat and eye-stripe of the adult being replaced by pale brownish.

In the nominate form of *Sphyrapicus varius* the adult male has red crown and throat, the mainly brownish (instead of black and white) juvenile male has no red but it usually moults some or all of the feathers on its forehead and crown before it attains other parts of the adult dress. The juvenile male of *S. thyroideus* has the same black and white colour pattern as the adult male but has a white instead of a red throat.

There appears to be only one published description of a juvenile male of *Campephilus principalis* (Tanner, in Bent, 1939). This bird resembled in colour the adult female and lacked the red nuchal crest of the male (which extends forwards on sides of head). It did not begin to show red feathers until it was about $3\frac{2}{3}$ months old. It is highly likely this is the normal situation and possible that some of the few other juveniles seen or collected, and sexed as females were, in fact, males also. It is also probable that the closely similar and possibly conspecific *C. imperialis* agrees with *principalis* in this.

(3) *Juvenile male has red (or yellow) on forehead and/or crown, adult male has this colour only on nuchal region.*

In this category are many species of *Dendrocopos*, one species (*rubiginosus*) of *Blythipicus* and, but to a marginal degree only, *Dendropicos fuscescens.* In this latter the red on the adult male's nape extends forward nearly to the crown.

(4) *Juvenile male has red on crown extending a little further towards forehead than red of adult male.*

In this category come all species of *Mesopicos* (3), both species of *Gecinulus* and, marginally, *Colaptes auratus* in which the juvenile male has a strong tinge of red on the crown.

(5) *Juvenile male and adult male both have red (or yellow) crown, this colour sometimes extending further over the nuchal region in the adult.*

This includes those species (many) of *Dendrocopos* in which the adult male has a red crown; *Mesopicos* (these come into category 4 also), *Thripias, Picoïdes, Dryocopus, Chrysocolaptes*; most species of *Dinopium* and *Picus*; some species of *Dendropicos* and some (possibly all?) species of *Veniliornis.*

(6) *Adult male has red only on malar region; juvenile male has red on forehead and crown also.*

Mulleripicus pulverulentus. I think it highly likely that the case is the same in *M. fuliginosus,* of which I have been unable to find either juveniles or descriptions of them. *Meiglyptes* may show a suggestion of this condition, some male juveniles being tinged with red on the forehead.

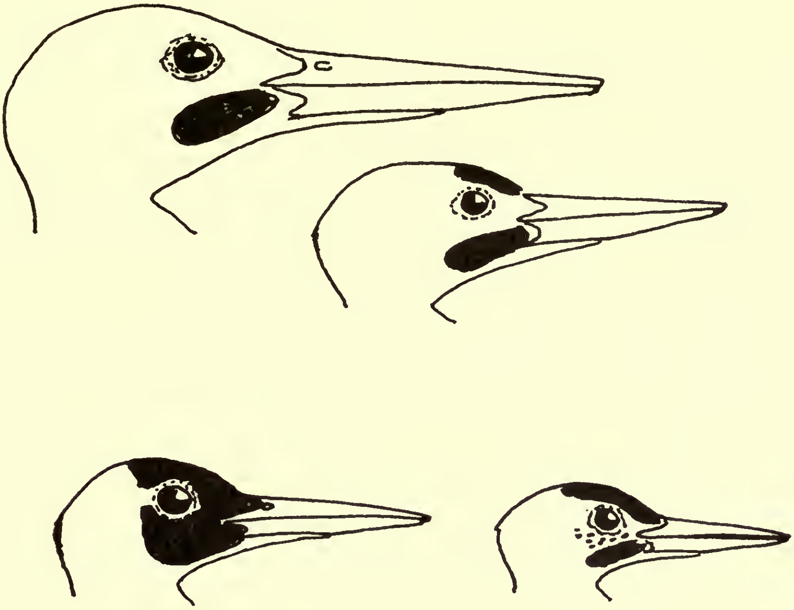

FIG. 4. Diagrammatic sketches to show colour patterns of heads of adult males (left) and juvenile males (right) of *Mulleripicus pulverulentus* and *M. fulvus*.

(7) *Juvenile female resembles adult female in having no red on head, in species in which males have red on head.*

Those species of *Colaptes* in which the males have red malar stripes; a few species of *Dendrocopos*, including the aberrant *D. albolarvatus*; some species of *Picus* (*squamatus* and its allies), *Meiglyptes*, *Chrysocolaptes* and *Dinopium* and in two related and rather aberrant species of *Campethera* (*nivosa* and *caroli*).

(8) *Juvenile female and adult female differ appreciably in colour of head but neither has any red although the male has.*

One species only, *Hemicircus concretus*, in which the adult female has the head (and most of the body) a concolorous olivaceous grey but the juvenile has the top of head and crest buff.

(9) *Juvenile female has some red (or yellow) on head; none present in adult female.*

Most species of *Dendrocopos*, *Picoïdes*, *Mesopicos*, *Thripias*, most species of *Dendropicos*, *Veniliornis callonotus* and, in all probability, other species of *Veniliornis* also.

(10) *Juveniles of both sexes have strikingly different coloration and colour pattern from adults.*

Melanerpes erythrocephalus. The juvenile appears predominantly greyish brown except on wings and tail owing to extensive pale brownish to brownish white fringes, central streaks and/or cross bars on the blackish cover feathers. There is only a little red around the eye, in contrast to the entirely red head of both sexes of the adult. The juveniles of the nominate form of *Spyrapicus varius* (and to a lesser extent those of other forms of the species) are very similar in general coloration (and in the plumage patterns by which this is achieved) to the juvenile of *M. erythrocephalus* described above.

Hemicircus concretus comes less definitely into this category. The colour pattern of the juveniles (but not their coloration) is very close to the adult male's (see Text-fig. 2) but they also show some indication of a buff malar stripe which is lacking in the adults.

(11) *Adults differ in coloration and colour pattern, juveniles very like respective adults but juvenile male lacks the red throat of the adult male.*

Sphyrapicus thyroideus. This species is of interest in that the differences between the male and female (at all ages) closely parallel the differences between adults and juveniles in the related *S. varius.*

(12) *Neither adults nor juveniles have red or yellow on head; juveniles resemble respective adults (allowing for very minor differences).*

Hemicircus canente. It seems probable that *Nesoceleus* comes into this category but I can find neither juveniles of this species nor descriptions of them.

The aberrantly coloured *Asyndesmus lewis* does not fit readily into any of the above categories. Its juveniles are similar to but generally duller than the adults. They lack the silver collar and upper breast, have only traces of red on the face and have white sub-terminal spots (not present in the adult) on the feathers of the hind neck.

DISCUSSION. Thus, taking the woodpeckers as a whole, juveniles tend to be less, although often only a little less, conspicuously coloured than the adults. Sexual dimorphism is usually present in the juvenile plumage but is often much less marked than in the adult plumage. In species in which the adult males or adults of both sexes have the head almost entirely red the juveniles (where known) have appreciably less red on the head. Juveniles, taking all species into consideration, approximate more closely to the familial mean in the amount of red on their heads than do adults. This is well exemplified, within a small genus, by *Mulleripicus pulverulentus* and *M. fulvus* (see Text-fig. 4) and certainly suggests that the juvenile colour pattern resembles a previous stage in the species' evolutionary history, as Voous (1947) claimed for the red crowns of those species of *Dendrocopos* which show this feature only in their juvenile plumage. Certainly speciation in woodpeckers has involved both reductions and increases in the red areas of the adult plumages.

It is likely, however, that many features of the juvenile plumages may be functional and hence of selective value. This seems obvious in *Melanerpes erythrocephalus* and *Sphyrapicus varius*, whose much less conspicuous juvenile plumage must give some protection against aerial predators; both these species are partly migratory and often inhabit relatively open, although wooded, country. Under such conditions it may be of great advantage to the inexperienced juveniles to be less conspicuous. The same is probably true for some other species in which the differences between young and adults are much less marked. In *Picus viridis*, for example, the more or less speckled and barred (but otherwise similarly coloured) juveniles are even less conspicuous when feeding on the ground than are the adults.

In the many species in which the juveniles are like the adults it is evident that here any advantages of a less conspicuous juvenile plumage are outweighed by others. Probably adult coloration is advantageous in the acquisition of territory or use of feeding areas in competition with adults. On the other hand the tendency in so many species, some of them congeneric with those showing strong sexual dimorphism, for the male and female juveniles to be almost alike, differing only in the female showing less extensive red or yellow areas than those of the male, may perhaps give other advantages which are more important for these species. It might, perhaps, lessen any tendency that might otherwise exist for either parent to " favour " young of one sex or it might better enable the female juvenile to hold her own in competitive strife with her brothers. Young *Dendrocopos major*, for example, may fight even in the nest hole (Sielmann, 1959). Where they are numerous, one sees much aggression and frequent fights between fledged young before (as well as after) they have moulted their juvenile plumage.

Where the juvenile lacks red on the head or has it more restricted than the adult it is tempting to suggest that this might function to reduce or inhibit aggressiveness on the adult's part, particularly in those species in which the juvenile lacks the red precisely on those parts, forehead and forecrown, which are presented to the adult when soliciting or taking food from it. This may be so but against this hypothesis is the fact that in some other species, including a large number of *Dendrocopos*, it is precisely these areas (forehead and forecrown) which are red in juveniles and not in the adult. It is often implied that the juveniles of those species of *Dendrocopos* that have a red nuchal patch have the entire top of the head red but in fact the young male, although having a red forehead and forecrown, is black on the nape where the adult male is red. The same is of course, true of the young female who has less red on her head (as a rule) than the young male. In these species of *Dendrocopos* the " replacement " of the red on the napes of adults by red on foreheads and crowns of juveniles reaches an almost bizarre state in the Red-cockaded Woodpecker *D. borealis* in which the adult male has a tiny red mark (the " cockade ") on the sides on the hindcrown and the juvenile male an equally small red mark in the middle of his forecrown. It is, of course, feasible that in some species some inhibition of adult agression could best be achieved by the young not presenting red markings to the feeding parent and in other species, in which the relative balance of fear and aggression differed, in their doing precisely that!

As *Dendrocopos major* is often instanced as a supposed example of a species in which the young are more brightly coloured that the adult it seems pertinent to digress here to say it is, in my opinion, very doubtful if the red foreheads of the juveniles make them more conspicuous to predators than are their parents. The same is probably true for the other species showing this character. All the boldly-marked black and white woodpeckers are, at least to human eyes, relatively conspicuous as compared with olivaceous or " ladder backed " species.

Section 2: Taxonomic notes on genera and species

MELANERPES, CENTURUS, TRIPSURUS AND LEUCONERPES

Peters (1948) included all the above genera in *Melanerpes* with the exception of *Leuconerpes*, which he retained as a monotypic genus for the White Woodpecker *candidus*. Hargitt (1890) had used a similarly broad conception of *Melanerpes* but had also included *candidus* therein. De Schauensee (1966) *retains the genus Leuconerpes* but notes that it "is perhaps not separable from *Melanerpes*." Selander & Giller (1963) give cogent reasons for treating *Tripsurus* as a synonym of *Centurus* but say that they do not feel justified in including both these genera in *Melanerpes*. However, I think that that is the most reasonable decision, unless all three genera are to be maintained. Both in its morphological characters and what is recorded of its ecology (see esp. Selander & Giller) *Tripsurus* seems perfectly to bridge the gap (such as it is) between *Centurus* and *Melanerpes* (sensu strictu). I provisionally maintain the genus *Melanerpes* as used by Peters, except as hereunder discussed.

The species *candidus* does not seem to me to be sufficiently distinct to warrent upholding the monotypic genus *Leuconerpes*. Its very distinct coloration, with entirely white head, parallels that of the few white-headed African barbets of the genus *Lybius*, the differences between most *Lybius* species and the white-headed forms being comparable to those between *candidus* and related species. Wetmore (1926) gave information on field habits of *candidus*, including its gregariousness (a feature also found in some *Melanerpes* species) and added that the genus *Leuconerpes* "in external characters . . . seems to be only slightly differentiated from *Tripsurus*." Sharncke (1931) concluded from studies of its tongue musculature that *candidus* was a primitive form and closely linked with *Sphyrapicus*. He found, however, several similarities between its tongue and that of *Melanerpes aurifrons*. Pending further and more detailed studies it is, I think, best to include *candidus* in the genus *Melanerpes*.

Melanerpes striatus

The Hispaniolan Woodpecker is a very distinct species which stands out among other species of *Melanerpes* by reason of its red rump, greenish yellow and black barred upperparts, yellow-green belly and, on closer investigation, its rather long tail and the marked sexual dimorphism in length of bill. For these and other reasons Selander & Giller (1963) argued that the monotypic genus *Chryserpes* should be used for this species. Later, however, after a detailed study of the species in the field in Hispaniola, the senior author (Selander, 1966) changed his opinion and was in favour of including it in *Centurus* (*Melanerpes*).

I do not know this species in life but on its museum characters I am entirely in favour of Selander's second decision. The barred pattern of its upperparts only differs essentially from other barred *Melanerpes* (*Centurus*) species in the greenish yellow instead of white on the paler parts of the feathers; this would seem to involve only the spread of lipochrome pigments to these areas. In this connection it may be significant that *M. superciliaris* from Cuba has the white parts of the mantle suffused with yellow and *M. radiolatus* from Jamaica has much dark yellow on the lower breast and belly. The head colour pattern of *striatus* is rather like that of *superciliaris*. Its largely yellowish green coloration gives *striatus* a certain resemblance to some species of *Chrysoptilus* but it shows no trace of the conspicuously barred and spotted underparts of these. The red patch on the rump is shared by no other New World woodpecker except *Veniliornis kirkii* but I do not think any of the *Chrysoptilus* species or *V. kirkii* are very close relatives of *striatus*.

M. flavifrons, M. formicivorus & M. chrysauchen

The Yellow-fronted Woodpecker *M. flavifrons* and the Golden-naped Woodpecker *M. chrysauchen* are allopatric and seem best given specific rank although they certainly comprise a superspecies. The differences of the colour patterns of the heads of these two are very similar to those between the North and Central American forms of the Acorn Woodpecker *M. formicivorus* and the South American form (*flavigula*) of that species. The differences between nominate *chrysauchen* from Costa Rica and the Pacific slope of western Panama and the race *pulcher* from northern Colombia may be in part or whole due to character displacement in reference to the different races of *formicivorus* with which they are sympatric (see Text-fig. 5).

Melanerpes rubrifrons

Peters (1948) gives the Red-crowned Woodpecker *rubrifrons* specific rank but others (Stresemann, 1924, Greenway & Griscom, 1941, Todd, 1946 & Haverschmidt, 1956) have concluded that is a colour phase (morph) of *M. cruentatus*. I fully agree with this latter opinion which is substantiated by the specimens in the B.M. collection. Besides phenotypically " pure " specimens of each form there are several that are intermediate, to varying degrees.

The African Woodpeckers

All the sub-Saharan African woodpeckers seem to be more closely allied to one another than to any non-African species or genus. They are, I think, representatives of the stock ancestral also to *Picus* and *Dendrocopos*. Adaptive radiation has, however, resulted in similar but less marked divergences to those shown by woodpeckers in Eurasia and America. The second possibility: that the African forms are polyphyletic, with *Thripias* and *Dendropicos* closer to *Dendrocopos*, and *Mesopicos* and *Campethera* to *Picus*, is, I think, rather less likely. In spite of some remarkable general resemblances in coloration I think that the South and Central American green woodpeckers are more closely related to other New World forms, in the genera *Colaptes* and *Melanerpes*, than they are to African forms. When comparing, for example, species of *Dendropicos* and *Veniliornis* that look much alike, one finds that some details of their colour patterns differ from each other and are, respectively, closer to those of other African and South American species.

There have been divergencies of opinion as to how many genera of African wood-

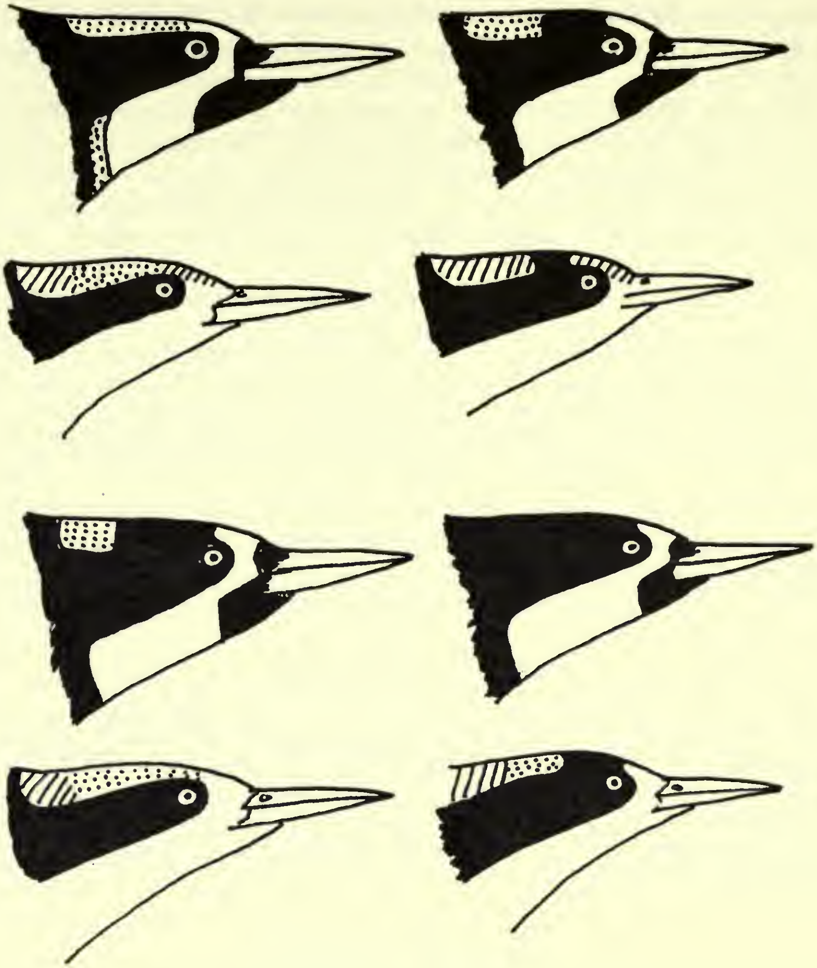

FIG. 5. Sketches to show colour patterns of heads of males (left) and females (right) of *Melanerpes formicivorus* (top) which overlaps in range with *M. chrysauchen* (second row) in Central America and of the form of *M. formicivorus* (third row) which overlaps with *M. chrysauchen* in northern South America. (See text).

peckers to recognize. Hargitt (1890) recognized the genera *Campethera, Dendropicos, Mesopicos, Thripias* and *Geocolaptes,* mainly on structural characters with emphasis on shape and size of bill. Other authors, notably Chapin (1939) recognized further genera but Mackworth-Praed & Grant (1957) followed Hargitt except for resurrecting the genus *Ipophilus* for the two species *obsoletus* and *stierlingi.* Peters (1948) put *elliotii* and *johnstoni* (now reckoned as a race of *elliotii*) in the genus *Polipicos* (following Chapin) but otherwise recognized the same genera as Hargitt and Praed and Grant although not with precisely the same allocation of species within them. I have followed Peters' nomenclature except where otherwise stated.

DENDROPICOS

Peters includes in this genus *fuscescens*, *stierlingi*, *elachus*, *abyssinicus*, *poecilolaemus*, *gabonensis* and *lugubris*. I concur with him in thinking that these species are probably more closely allied to each other than any is to species in another genus. This assumes, as I think is likely, that some differences of general coloration such as a tendency towards light, barred or spotted plumage in dry savannahs; darker, greener coloration in forests and the acquisition of a red rump have arisen independently in different (but related) stocks.

Their head markings suggest the *Dendropicos* species are nearer to *Thripias* and *Mesopicos* than to *Campethera*. The extreme similarity between *Dendropicos lugubris* and *Campethera nivosa* is, I think, due to parallel development but it may indicate true affinity in spite of differences in bill shape.

" *Dendrocopos* " *obsoletus*

Most writers on African woodpeckers (Bates, 1937, Chapin, 1939, Hargitt, 1890, Peters, 1948, Voous, 1947) put the Brown-backed Woodpecker, *obseletus*, in the genus *Dendrocopos* (or in *Yungipicus* which is now usually regarded as a synonym of *Dendrocopos*) but Grote (1928) and Bannerman (1933) placed it in *Dendropicos*. Voous in his monograph on *Dendrocopos* says that Grote and Bannerman had " abusively referred (it) to *Dendropicos* " and adds that this latter genus is quite distinct in having reddish or yellowish shafts to rectrices or remiges and usually in addition a distinct greenish tinge of the plumage. He considered, however, that *stierlingi* was correctly referred to *Dendropicos*. Mackworth-Praed & Grant, 1957, place *obsoletus* and *stierlingi* together in the genus *Ipophilus*.

I think that Bannerman and Grote were right to include *obsoletus* in *Dendropicos*. Among them the *Dendropicos* species show varying amounts of green coloration and/or yellow or reddish quill shafts. In two of them, *stierlingi* and *elachus*, this is reduced to a not very pronounced yellow tinge in the shafts of the wing and tail quills (*stierlingi*) or tail quills only (*elachus*). If either of these two species are compared with any other *Dendropicos* species it will be seen that the " gulf " between them, so far as yellow pigmentation is concerned, is greater than that between either one of them and *obsoletus*.

Voous links *obsoletus* with the pygmy woodpeckers of south Asia, *Dendrocopos nanus* and its allies, but in plumage pattern *obsoletus* is closer to *Dendropicos* species than it is to any of the Asian forms. In its coloration it is nearest to *elachus* although it lacks the latter's scarlet rump which is, in all probability, a species recognition mark serving to isolate *obsoletus* and *elachus* in the areas where their ranges overlap. Such species as *obsoletus* and *elachus* undoubtedly indicate the close relationship between " green " and " pied " woodpeckers or the potentiality for " green " and " pied " forms to evolve, in different geographical regions, from a common stock. I think, however, there is little doubt but that the true affinities of *obsoletus* are, as Bannerman and Grote decided, with *Dendropicos*.

Campethera bennettii, C. scriptoricauda & C. nubica

Benson (1952) gives evidence for the conspecifity of Bennett's Woodpecker *C. bennettii* and the Tanganyika Woodpecker *C. scriptoricauda*. In *C. bennettii vincenti* (Grant & Mackworth-Praed 1953) the throat colour of females is intermediate between the chocolate brown of *bennettii* and the creamy white of *scriptoricauda*, although it does not have the black spots of the latter. Some males of *vincenti* also have the ear coverts a less pure white than those of other forms of *bennettii*. Also a female *scriptoricauda*, from Blantyre, shows some approach to *bennettii* in colour, having fewer and smaller spots than usual, on a beige-tinted throat. It is unlikely that these specimens merely indicate occasional hybridization between two " good " species as there seem to have been no " pure " specimens of either *bennettii* or *scriptoricauda* collected within the range of *vincenti* and, more importantly, Mr Benson informs me (pers. comm.) that the calls and ecology of *bennettii* and *scriptoricauda* do not differ. I therefore agree with him that, on present evidence, *scriptoricauda* is best considered as a race of *bennettii*.

The very distinctive chocolate and white markings on the face and throat of the females in most forms of *bennettii* and, possibly, also the very white cheeks and intense red malar stripes of the male, probably function as isolating mechanisms in reference to *C. abingoni*, with which the chocolate-throated forms of *bennettii* overlap widely in range whereas *scriptoricauda* (and *C. nubica*) overlap only marginally with *abingoni*.

The Nubian Woodpecker *C. nubica* does not seem to differ in any significant plumage character from *C. bennettii scriptoricauda*; they differ only in the unspotted throat of *nubica*. Localities of specimens in the British Museum collections do not suggest any actual overlap of distribution. I provisionally maintain them as separate species, however, because Mr. C. W. Benson informs me that their calls differ, or at any rate those calls most usually uttered, and they differ in ecology.

Campethera nubica & P. punctuligera

I provisionally treat the Nubian and the Fine-spotted Woodpeckers, *nubica* and *puctuligera*, as members of a superspecies but I think it likely that they may prove to be conspecific. Although their respective ranges come close together in the southern Sudan and the eastern Congo I can find no evidence of both having been taken or identified in the same area (see also Chapin, 1939).

The form of *punctuligera*, *C. p. balia*, from the south-eastern Sudan and eastern Congo is largely intermediate in colour and colour pattern. The differences between the two forms are, chiefly, the size and formation of the spots on the breast and the presence (in *punctuligera*) or absence (in *nubica*) of spotting on the throat. One female of *balia* from Baginzi, Bahr el Gazal (B.M. No. 1919.10.7.23.) comes closer to *nubica* than most, having no spots on the throat, very dull underparts (less yellow tinge than usual in *punctuligera*) with the breast spots closely approaching those of *nubica* in pattern and general appearance although still much smaller than those of *nubica*. A juvenile from Angba, on the river Welle, also much resembles *nubica* in its breast spots.

Chapin (1939) says that the calls and habits of *punctuligera* and *nubica* are extremely similar and that "adherents of the Formenkreise theory" would surely consider them as forms of one species. A main difficulty and the one that chiefly prompts me still to treat them as species is that in appearance *punctuligera* could equally well be a form of *bennettii*, with which it is also allopatric. In fact there is an even closer resemblance in colour pattern between *punctuligera* and *bennettii scriptoricauda* than between the former and *nubica*. Present evidence suggests differences between the calls of *bennettii* and those of *scriptoricauda* but this negative evidence is of no great significance until the vocalizations of all three forms have been recorded in more detail. I suspect they may prove all to be members of a superspecies or even conspecific.

Campethera notata

I think Clancey (1958) is, right in suggesting that the Knysna Woodpecker *notata* and the Golden-tailed Woodpecker *abingoni* are possibly conspecific and certainly members of a superspecies. In spite of their great similarities, however, the pattern of the breast spots in *notata* is closer to those of *nubica*, *bennettii* and *punctuligera*, with none of which is *notata* sympatric, than to *abingoni* although such breast spots as those of *notata* could easily drive from the streaks of *abingoni* or *vice versa*.

Campethera cailliautii, C. taeniolaema & C. maculosa

These three species are all very closely allied, the Little Spotted Woodpecker, *cailliautii* and the Fine-banded Woodpecker *taeniolaema* being mainly allopatric. Their ranges overlap in the eastern Congo and adjacent areas where they appear, however, to be ecologically isolated, *taeniolaema* inhabiting the highlands and *cailliautii* the lowlands. They are very similar in coloration but *cailliautii* has the throat and face buffish with blackish, speckly-looking, barring whereas *taeniolaema* has the face and throat greenish white very finely barred with greyish olive.

From the Golden-backed Woodpecker *maculosa*, with which it is sympatric, *cailliautii* differs in the male having a slightly brighter red crown, greener and les gold-tinged upperparts and less boldly spotted on the throat. The females differ rather more markedly in *maculosa* lacking the red nape of *cailliautii*; she also has her entirely blackish crown spotted with deep buff, the spots on the head of *cailliautii* being pale buffish to white.

Campethera tullbergi

The rather distinct Tullberg's Woodpecker appears to be closest to *cailliautii* (*permista*) with which it is sympatric. The carmine patch on the carpel area of the wing probably serves as a species-specific recognition mark in reference to *cailliautii*. I fully concur with Peters (1948) that *C. wellsi* should be considered a race of *tullbergi*.

Campethera nivosa

The Efulen race of the Buff-spotted Woodpecker, *efulensis* Chubb, appears to be inseparable from nominate *nivosa*. One of three specimens from the type locality

(*Efulen, Cameroon*) can be matched by a specimen of *nivosa* from Portuguese Guinea. The large series from Kumba, Cameroons, vary from typical " *nivosa* " to typical " *efulensis* " in colour. The races *poensis* and *herberti* are slightly differentiated but recognizable.

MESOPICOS

The Grey Woodpecker *M. goertae* and the Olive Woodpecker *M. griseocephalus* are very closely related and could certainly be considered as members of a superspecies or even as conspecific but for the fact that their ranges overlap in parts of Kenya and north-eastern Tanzania. We have, however, no records of both species from precisely the same place although there are specimens of both from north-eastern Tanzania, *goertae* from Nabara and *griseocephalus* from Same. In and near the area of apparent overlap they appear to be ecologically separated, *griseocephalus* being confined to highland forest.

The only absolute colour differences between the adults are the darker grey head and golden-olive breast of *griseocephalus*. In *goertae* juveniles of both sexes have red on the head, the male usually rather more than the female. Some works on African birds imply that in *griseocephalus* the young are, except for being duller, like the respective adults. There are only six juvenile *griseocephalus* in the British Museum collection, some unsexed, others sexed as males. All of them have red on the head; in some of them the red is less extensive than in others and I suspect these may be females. Juveniles of *griseocephalus* are, incidently, paler and greyer in colour than adults and thus come even closer to *goertae* in appearance than do the adults.

A few remarks on geographical variation in both species: From West Africa (Senegal, Gambia, etc.) across to Uganda and the southern Sudan *M. goertae* shows no striking differentiation, if allowance is made for individual differences (from the same area some birds may have an orange-red belly patch and others not) and those due to wear (which are often considerable). Within this region there is a tendency for birds from the more northern arid areas to be palest and to have more distinct barring on the wings and upperparts, those from the southern areas to be darker and duller. Specimens from Gambia to Uganda tend to have little or no orange-red, only yellowish, on the belly. Those from the extreme north-east of this area (parts of Southern Sudan) are *more* like those of Senegal in coloration than are the latter to Gambian birds!

I think it best to recognize three races within the above areas: nominate *goertae* from Senegal, the paler *königi* (Neumann, 1903) from the Lake Chad regions, parts of French Niger and French Sudan and *centralis* (Reichenow 1900) and agree with Mackworth-Praed & Grant (1957) in thinking *agmen* (Bates, 1932) and *oreites* (Grote, 1923) best treated as synonyms of *centralis*. This is an admittedly wide but I think workable interpretation of *centralis* but it must be borne in mind that no hard and fast line can be drawn between any of the above-mentioned forms of *goertae*. To the east of its range *centralis* intergrades with *abessinicus* (Reichenow, 1900).

M. griseocephalus persimilis (Neumann, 1933), described from the Highlands of

Angola (Benguella) was recognized by Peters but has since been commonly treated as a synonym of *ruwenzori* (Sharpe, 1902). In the original description *persimilis* was separated on its smaller size. Besides the rather slight size difference our specimens from Angola, southern Congo and Tanzania mostly show quite conspicuous paler barring on the flanks which is absent from specimens of *ruwenzori* from Ruwenzori and Lake Kivu. I have, therefore, recognized *persimilis*.

Mesopicos elliotii

Chapin (1939) & Peters (1948) both use the genus *Polipicus* Cassin for Elliot's Woodpecker which was previously (Hargitt, 1890) and subsequently (Mackworth-Praed & Grant, 1957) included in *Mesopicos*. In structure of bill *elliotii* (with which *johnstoni*, formerly given specific rank, is now reckoned conspecific) is nearer to *Mesopicos* than to other African genera but in its other external characters it seems to be as close to *Campethera*. The two genera are, however, closely allied. It seems preferable to leave *elliotii*, at least provisionally, in *Mesopicos* rather than to place it in a monotypic genus.

Mesopicos elliotii sordidatus (Bates, 1928) was described from a juvenile from Oku, west of Kumbo, Cameroons. Its supposed racial characters are merely those of the juvenile plumage. There are now two adults from Oku in the British Museum collection, these do not differe from examples of *M. e. johnstoni* of which I therefore consider *M. e. sordidatus* a synonym.

THRIPIAS

Peters (1948) includes the Bearded Woodpecker *namaquus*, the Fire-bellied Woodpecker *pyrrhogaster* and the Golden-crowned Woodpecker *xanthocephalus* in the genus *Thripias*. Many other authors, e.g. Hargitt (1890), Chapin (1939) and Grant & Mackworth-Praed (1957) have put *pyrrhogaster* and *xanthocephalus* in *Mesopicos*, presumably mainly on account of their proportionately shorter wings (than those of *namaquus*) and maintained *Thripias* as a monotypic genus.

I think Peter's arrangement is best. These three species all agree in having a relatively long and straight bill, black nuchal region in both sexes and similar characteristic facial markings. Against these I do not think that the proportionately longer bill and tail of *namaquus* warrants its generic separation. *T. namaquus* seems to link the other two *Thripias* species (as reckoned here) with *Campethera* rather than with *Mesopicos*. In this connection it may be mentioned that the female of *Campethera bennettii* has facial markings rather similar to, although not identical with, those of the *Thripias* species.

Geocolaptes olivaceus

I think the Ground Woodpecker is most closely related to other African forms and that its resemblance to some of the American flickers, *Colaptes*, (near which it is usually placed in systematic lists,) is due to convergent adaptations for terrestial or semi-terrestial life. It differs from the *Colaptes* species but very closely resembles

Mesopicos goertae and *M. griseocephalus* in colour pattern except for the barred tail and the vestigial red malar stripes of the male. Both these are, however, very widespread characters in " green " woodpeckers and occur, *inter alia*, in some *Campethera* species.

It seems likely that *olivaceus* evolved from some form ancestral both to itself and to *goertae* and *griseocephalus*. It may well have retained (or developed) red malar stripes as a species-specific recognization mark in reference to *griseocephalus* (or its ancestor). The present apparently obsolescent state of the malar markings might indicate that the development of greater divergence in size and ecology has now obviated the need for such distinguishing markings between these two forms.

Notes on ***Picus***

Peters (1948) includes in *Picus* the former genera *Chrysophlegma*—species *mentalis* and *flavinucha*, and the monotypic *Callolophus*—species *mineaceus*. Hargitt (1890) included the latter in *Chrysophlegma* also although he placed the smaller yellow-crested forms, *puniceus*, *chlorolophus* and *chlorigaster* with the " typical " green woodpeckers in the genus *Gecinus*. Within Peter's broad and inclusive conception of *Picus* the species fall into three rather distinct groups which are not precisely the same as those suggested by former allocations of species between *Gecinus* (or *Picus*) and *Chrysophlegma*. The latter genus was defined as having " wing rounded . . . nasal ridge almost obsolete, culmen ridge very blunt, tail two thirds length of wing " and later by Stuart Baker as having " . . . bill more curved and nasal ridge almost obsolete, well-developed nuchal crest. " These definitions have, apparently, restrained those who recognized *Chrysophlegma* from including in it the species *chlorolophus chlorigaster* and *puniceus*, which have rather straighter culmens that the other yellow-crested species.

The group of most typical *Picus* species comprises *viridis*, *canus*, *vaillantii*, *awokera*, *viridanus*, *vittatus*, *squamatus*, *xanthopygaeus*, *erythropygasus and rabieri*. All these are relatively long-billed forms with fairly straight culman, nuchal crest absent or slight, primaries marked whitish and black or grey, and except in one race of *canus*, no red or chestnut colour on wings. *P. rabieri* has a more rounded wing and rather shorter bill than the others and approaches the next group in these features.

The species in the second group are characterized by having yellow nuchal crests, shorter bills and, one species excepted, red coloration or at least a reddish tinge, on the wings. They comprise *flavinucha* and *mentalis*, which in addition to the characters listed above also have black and chestnut primaries and a spotted patch on the throat, and *puniceus*, *chlorolophus* and *chlorigaster* which have rather straighter culmens, no chestnut on their primaries which are dark and whitish, varying amounts of red on the head, and are smaller in size. To some degree these three forms link the original " *Chrysophlegma* " species to the first group but they are, I think, much more closely allied to the former.

The third group consists of the single species *mineaceus*. This has a long and broad occipital crest, relatively short, broad bill, barred plumage pattern both above and below and rather harsh, coarse-feeling plumage. Although it may be justifiable to include *mineaceus* in the present enlarged conception of *Picus*, (and certainly this is more reasonable than allying it with *flavinucha* and *mentalis* and yet not putting *puniceus*, *chlorolophus* and *chlorigaster* in the same genus), it is a very distinct species. It appears to be a link between *Picus*, via *Picus puniceus*, and the Rufous Woodpecker *Micropternus* to which it shows some approach in proportions, coloration, plumage pattern and plumage texture.

I think it possible that more comprehensive studies might indicate that the species in this second group are less closely allied to those in the first group than are the latter to such Ethiopian genera as *Campethera* and *Mesopicos*.

Picus canus

In the eastern part of its range, where it and *viridis* do not overlap, the Grey-headed Woodpecker *canus* much more nearly approaches the Green Woodpecker *viridis* in size and proportionate length of bill. The only similarly-sized green woodpeckers which it overlaps in eastern Asia are *P. erythropygius* and *P. rabieri*, which are very distinct from *canus*, with striking colour differences. *Picus dedemi* of Sumatra seems rightly put as a form of *canus* in spite of its different colouring, with bronzy carmine, with a hint of green, replacing the green and olive of *canus*. The racial variation within the Paleartic populations of *canus* has been very fully discussed by Vaurie (1959).

Picus vaillantii

Vaurie (1965) put North African Green Woodpecker *vaillantii*, as a race of *viridis* and earlier (1959) anticipated this decision on the grounds that in everything except the black malar stripe of the male, which he considered an " alternate character " to the red and black malar stripe of the male *viridis*, *P. viridis sharpei* of the Iberian peninsula " bridges the gap " between *viridis* and *vaillanti*. He pointed out *vaillantii* had already been listed as conspecific with *viridis* by Goutenoire (1955) and that Dr. David Snow, who has observed this species in the wild, was also in favour of this decision.

I cannot, however, see that *sharpei* is intermediate between [other races of] *viridis* and *vaillantii* except in bill shape and I do not think that minor details of size, size of bill or tone of general colour, in all of which *vaillantii* comes nearer to *viridis* than it does to European forms of *canus*, are of much significance when dealing with a geographically isolated " green woodpecker ". Especially in view of the amount of geographic variation shown by both *viridis* and *canus* and the obvious close relationship of the above three forms and the Japanese Green Woodpecker *P. awokera*. The female of *P. viridis sharpei* has the feathers of the forehead and crown red (or, to be more precise, these areas all tipped with red) as in other races of *viridis*, whereas these areas are without any red in females of *vaillantii*. Incidently, the red tips on the nape feathers of *vaillantii*, appear longer than and somewhat different in texture from those of *viridis* or *canus*.

While *vaillantii* may be more closely allied to *viridis* than it is to *canus* or *awokera*, the differences in colour patterns of their heads, lack of red on malar stripe of male *vaillantii* and black and grey instead of red forehead and crown of female, might be

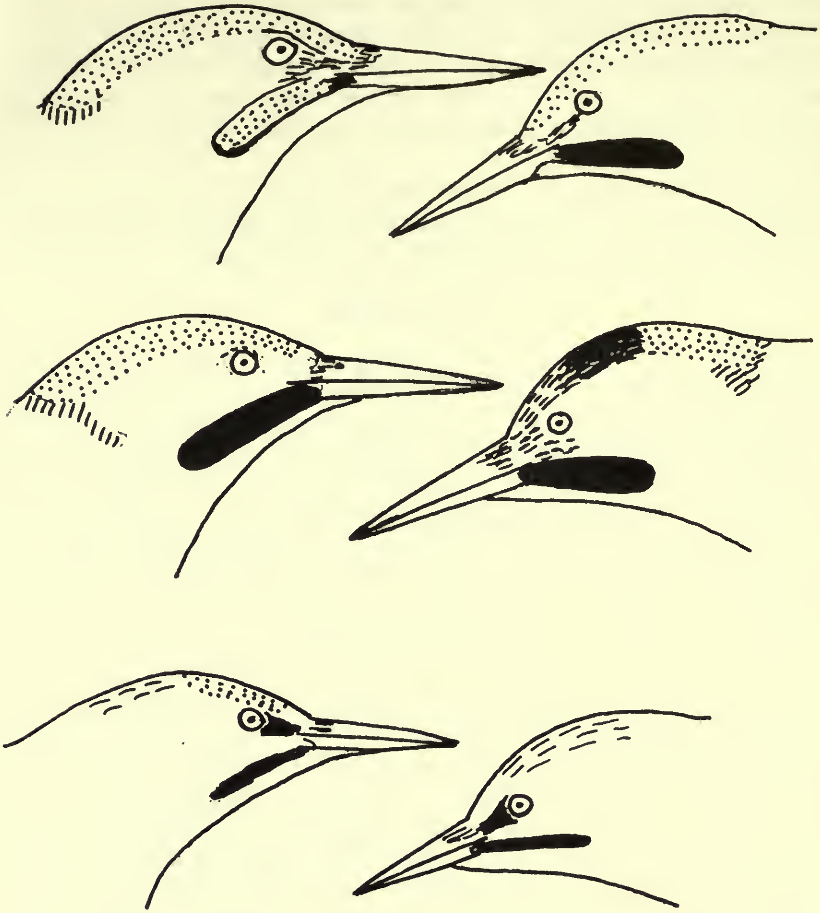

FIG. 6. Diagrammatic sketches to show colour patterns of heads of males (left) and females (right) of *Picus viridis* (top, *Picus vaillantii* (middle) and *P. canus* (bottom).

pre-adapted to act as isolating mechanisms should the two ever overlap in range. Of its more striking plumage characters *vaillantii* shares one (crown and nape of male red) with *viridis*, two (no red on malar stripe of male, forehead and crown of female grey or grey and black) with *canus* and two (red on nape only of female, forehead and crown of female grey or black and grey) with the more geographically distinct *awokera*. I think it best, therefore, to give *vaillantii* specific status although it can, at least provisionally, be put in the same superspecies as *viridis*.

Picus rabieri

This is a very distinct species but, in spite of its rounded wings and somewhat different colour pattern, I think it is an offshoot of the *viridis* group although in wing shape and in its rather short bill it shows some approach (convergence) towards the *flavinucha* group.

Picus squamatus, P. viridanus, P. vittatus & P. xanthopygaeus

These species form a closely related group and are essentially alike in coloration and colour pattern. The Red-rumped Woodpecker *P. erythropygius* is related to this group, as its colour pattern especially in the eye-striped morph, clearly indicates.

The Scaly-bellied Green Woodpecker *P. squamatus* overlaps in part of its range with the Little Scaly-bellied Woodpecker *P. xanthopygaeus* from which it differs in being much larger, having very conspicuous black and white malar stripes, the upper breast plain greyish green without squamate markings and conspicuously barred central (and other) tail feathers.

P. xanthopygaeus overlaps with the Burmese Scaly-bellied Woodpecker *P. viridanus* and marginally with the Laced Green Woodpecker *P. vittatus* from both of which it differs in having inconspicuous (almost obsolescent) malar stripes, more streaked (longitudinal squamate markings) throat and yellow or greenish yellow instead of yellowish green rump and upper tail coverts.

P. vittatus and *P. viridanus* are extremely similar, differing in appearance only in *viridanus* having the streaky-looking squamate markings of the underparts extending forward onto the upper breast and throat where they are, however, less clearly defined than lower down. As given in many standard works the ranges of the two would appear to overlap in parts of Eastern Burma and south-western Siam. In the fairly extensive series of both in the British Museum (Natural History) there are no specimens of both species from any one area with the exception of one specimen of *viridanus*, allegedly from Tenasserim, where only *vittatus* normally occurs. I think this probably represents some error in labelling.

Robinson & Kloss (1923) say that " where the ranges of the two species touch or approach there is not the slightest sign of intergradation ". In view of the extremely slight differences between them I do not find this statement very convincing. There are two specimens in the British Museum, No. 1887.8.10.1556 from Mergui and No. 1887.11.1.95 from " Burmah ", which are absolutely intermediate between " typical " *vittatus* and *viridanus* at first appearance. On closer examination they are seen to have squamate markings on the upper breast although these are fainter than usual in *viridanus*. It is significant, perhaps, that in all specimens of *viridanus* these squamate markings are least developed on the upper breast and throat, contrary to what one might expect if they functioned as a species recognition mark in reference to *vittatus*.

Deignan (1963) puts *viridanus* as a race of *vittatus* and, although he does not there give his reasons for so-doing, all the evidence I have been able to find suggests that he is quite right in this decision.

Picus chlorolophus & P. chlorigaster

The number of races of the Small Yellow-naped Woodpecker *chorolophus* that has been described tends to obscure the main difference which is between the populations in peninsular India and Ceylon and those from elsewhere. The former, at one time given specific status as *P. chlorigaster*, are not only geographically isolated but in some characters come closer to the related Crimson-winged Woodpecker *P. puniceus* resembling it and differing from typical *chlorolophus* in having blackish lores, instead of whitish as in *chlorolophus*, and the top of the head entirely red. In the amount of red on their wings they are intermediate.

The three forms, *chlorigaster*, *chlorolophus* and *puniceus* are allopatric except that an isolated race of *chlorolophus* (*rodgeri*) occurs in the mountains of Perak. There is thus a very limited geographical overlap of this form with *puniceus* although there is apparently no ecological or altitudinal overlap (Robinson, 1928). This montane race is rather dark in colour and thus superficially somewhat intermediate between *chlorolophus* and *chlorigaster* but in its main features it agrees with the former, with which its affinities clearly lie. I think it is preferable to treat *chlorigaster* as a member of a superspecies, together with *chlorolophus* and *puniceus*, rather than as a race of *chlorolophus*.

DENDROCOPOS

Voous (1947) shows that the American and Asiatic " ladder-backed " woodpeckers in this genus all inhabit areas that were not covered with Pleicestocene land-ice and which, in North America, represent the glacial forest refuges. He considers all these ladder-backed species to be (relatively) closely related in spite of their present discontinuous ranges.

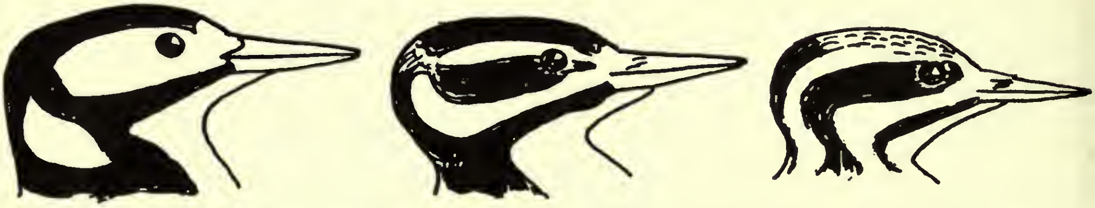

Fig. 7. Diagrammatic sketches to show colour patterns of heads of a typical Old World *Dendrocopos* (*major*), a typical New World ditto (*villosus*) and *Picoïdes trydactylus* (left to right) (In all species the heads shown are of females).

All American ladder-backs agree with other American *Dendrocopos* species, and differ from most Old World *Dendrocopos* species, ladder-backed and otherwise, in lacking red on the ventral regions or under tail coverts. They also have a similar head pattern, with a dark post-ocular band, to other American *Dendrocopos* species. I think these facts indicate that all the New World *Dendrocopos* species are more closely related to each other phylogenetically than any one of them is to any Old World form.

It seems more likely that the " ladder-back " pattern (so common in woodpeckers generally) has developed, or been retained if it was a primitive feature, independently in both Old and New Worlds, as an adaption to relatively open or well-lighted habitats in which it probably has protective value, than that some factor in the American environment has caused two or more phylogenetically distinct *Dendrocopos* stocks to lose all trace of red on the underparts and to acquire similar facial markings subsequent to their arrival in America. In this connection it is pertinent that in some species of *Melanerpes* the adults are plain backed and the juveniles ladder-backed and in the Three-toed Woodpecker *Picoïdes tridactylus* some races are ladder-backed and others not (see Text-fig. 8).

Of Old World species the " dwarf " woodpeckers, *D. minor, D. kizuki, D. nanus et al.*, come nearest to the American forms in their colour patterns and are, I think, closest to them phylogenetically.

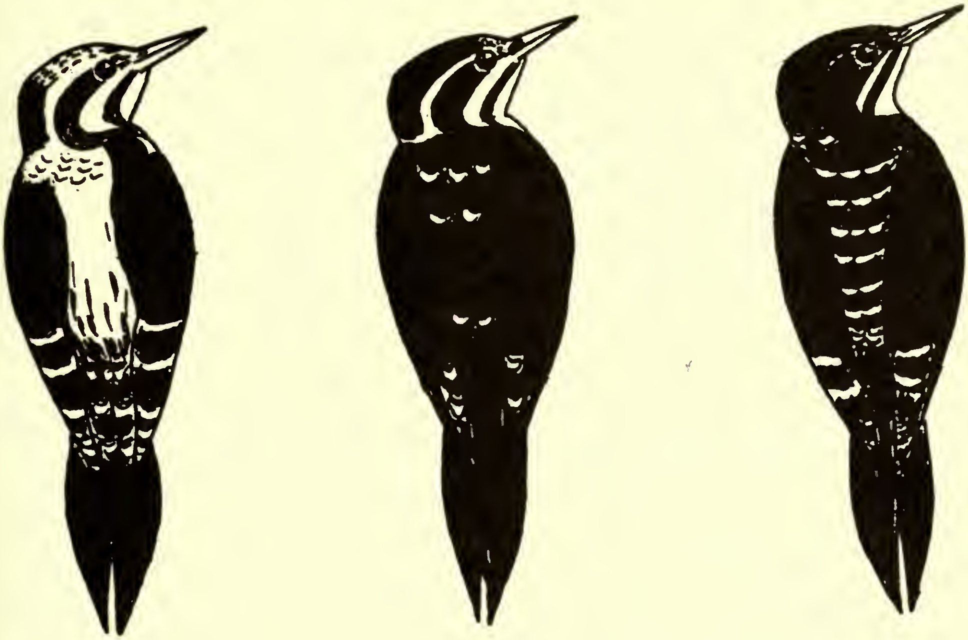

FIG. 8. Diagrammatic sketches to show variation in back pattern within a species: Females of *Picoïdes trydactylus* from Sweden (left), South-eastern Tibet (middle) and eastern North America (right).

The Hairy Woodpecker *D. villosus* and the Downy Woodpecker *D. pubescens* are now very largely sympatric. They presumably derived from a common ancestor at a relatively recent date as their colour patterns are virtually identical. They also show similar geographical variation although this, by itself, is of course, no argument for close relationship.

Nuttall's Woodpecker *D. nuttallii* and the Cactus Woodpecker *D. scalaris* are also close relatives. They appear not to be sympatric and descriptions of their calls do not suggest any great difference of voice. They may prove to be conspecific but provisionally are, perhaps, best treated as members of a superspecies. The Red-cockaded Woodpecker *D. borealis* is, I think, closely allied to them. Its strikingly different facial pattern seems to have been achieved by the extreme reduction of the usual (in American *Dendrocopos*) black post-ocular stripe so that only a vestige of this marking remains. I think, however, that the great similarity in position and extent of the red on the head in this species and the Old World *D. kizuki* is due to convergence, within related stocks, and does not indicate that *borealis* is closer to *kizuki* than are other American species. The juveniles of *borealis* and *kizuki* do not, apparently, resemble one another in position of red on the head as *kizuki* is said to resemble the adult in this respect. The Arizona Woodpecker *D. arizonae* and Strickland's Woodpecker *D. stricklandi* are allopatric, they are close to one another in appearance, voice, behaviour and ecology (Davis, 1965). On its upperparts *stricklandi* has a colour pattern intermediate between that of completely ladder-backed species and those, such as *arizonae*, with uniform dark back and rump. Individuals of *arizonae* which show traces of a barred dorsal pattern do, however, occur (Davis, 1965). The two are otherwise similar in colour but differ in *stricklandi* having dark streaks on the underparts with some indication of barring on the flanks, whereas *arizonae* is spotted, but the differences are less impressive when the markings on the individual feathers are compared. I think *arizonae* and *stricklandi* are best considered members of a superspecies.

The two South American forms the Striped Woodpecker *D. lignarius* and the Chequered Woodpecker *D. mixtus* differ from all North American *Dendrocopos* species in having their central tail feathers strongly barred with white and they are generally lighter and more " spotty " in appearance. They show much resemblance in plumage pattern to *Veniliornis spilogaster* and I think this may indicate close relationship between *Veniliornis* and *Dendrocopos*. They agree, however, with the northern forms in general overall colour pattern. From their visual characters one would certainly suspect them of being conspecific but they apparently overlap in range, both being found in Nequen and the eastern Rio Negro in Argentina (Peters, 1948, Olrog, 1963). Two specimens in the British Museum from Cordova, Argentina, (B.M. Nos. 1889.2.26.112 and 113) appear to be intermediate between *D. lignarius* and *D. mixtus berlepschi*. The male of the two agrees with *mixtus* in the extent of the red on its head but both are closer to *lignarius* in plumage pattern, which is, however, extremely similar in the two species (?) in any case. These two have longer bills than our specimens of *berlepschi* but we have only two of the latter and, at least in *lignarius*, this feature seems prone to individual variation.

The White-headed Woodpecker *Dendrocopos albolarvatus* is rather aberrant in colour pattern and its tongue is said (Voous, 1947) to be less extensible than in other (all other?) *Dendrocopos* species. Its external features, particularly the typically dendrocopine correlation of a red nape in the adult adult male with a red crown and black nape in the juvenile indicate that Peters was right to include it in *Dendrocopos*.

Dendrocopos darjellensis

Measurements of our specimens seem to indicate a less clear-cut difference between nominate specimens of the Darjeeling Pied Woodpecker, *darjellensis*, and *D. darjellensis desmursi* (J. Verreaux) than did those measured by Vaurie (1959) We have, however, no topotypical specimens of *desmursi* from Sikang and only a few from Yunnan. Our only specimen of *fumidus*, from the Naga Hills, does not show the characters claimed for this race (Ripley, 1951) and thus tends to confirm Vaurie's opinion that *fumidus* should be considered a synonym of *darjellensis*.

This species overlaps widely with the Crimson-breasted Pied Woodpecker

D. cathpharius. The two are nearly identical in coloration but differ much in size. Their yellow-tinged cheeks and underparts, red breast bands and heavy streaking on the underparts are considered by Voous to be primitive characters. Whether this is so or not these characters might function now as species-specific signal markings.

Dendrocopos leucopterus

I concur with Voous (1947) and Vaurie (1959) in thinking that it is better to give *leucopterus*, provisionally, specific rank. This, however, is mainly on grounds of convenience. I think Vaurie has rather over-emphasised the differences between *leucopterus* and *major*. I have seen no juvenile specimens of *leucopterus* so do not know if I should think them so distinct from juvenile *major* as they are said to be. It seems, however, pertinent to remark that although, as Vaurie says, juvenile *major* of both sexes have red on the crown, that on the female is normally less extensive than the male's. So the fact of the juvenile female of *leucopterus* having (always?) an entirely black crown may not be of specific significance.

Dendrocopos dorae

Although at first glance the Arabian Woodpecker is rather like some of the species in the African genus *Dendropicos* it seems most closely allied to the Eurasian forms of *Dendrocopos* and is now rightly included in that genus.

I think that *dorae* may be closest to *medius*; to which it bears much resemblance when allowance is made for " fading " of the black areas to darkish brown (already often shown to some extent in some individuals of *medius*) and for reduction of the white areas. In size, texture and colour of the red crown feathers, and the streaking on its flanks it is very like *medius*. Indeed, the differences between these two woodpeckers are very similar in kind, although greater in degree, to those between the Arabian form of the Magpie *Pica pica* and its more northerly representatives. In *dorae*, like most *Dendrocopos* species but unlike *medius*, the female lacks red on the head but I do not think this feature of *medius*, which is unique within the genus, argues against their close relationship. *D. medius* and *D. leucotos* are unquestionably close relatives, but differ in this feature as they do in size and bill shape.

Dendrocopos analis, *D. atratus* & *D. macei*

I provisionally follow Peters & Deignan (1945) in treating *analis* as a form of the Fulvous-breasted Pied Woodpecker *macei*. They differ slightly in size, in *analis* having a spotted rather than a streaked breast, white ground colour on underparts and central tail feathers and upper tail coverts barred with white instead of uniformly black. They do not, however, differ in colour pattern of the head. Intermediates occur (*fide* Deignan, 1945) in the Chiang Mai area of Siam.

Voous (1947) suggests that *macei* and the Stripe-breasted Pied Woodpecker *atratus* may be conspecific, quoting Standford & Ticehurst (1939) that where they appear geographically to overlap in range in northern Burma *macei* is a lowland and *atratus* a highland form. He mentions specimens of *macei* obtained by Hume in Manipur, Assam and implies that these showed some intergradation with *atratus*.

At least some of these Manipur specimens are in the British Museum collection and do not seem to differ from other specimens of *macei*, collected elsewhere. When they are compared with specimens of *atratus*, also collected in Manipur, the differences between them are at least as great as between specimens of both from elsewhere. That is, *macei* differs in being smaller, having an unstreaked lower throat, the underparts creamy rather than dusky yellowish and with not very prominent dark streaks, as against very prominent dark streaks in *atratus*. The red on the ventral region does not usually extend so far forwards, the red of the head is a little less bright and the red feathers are a little dissimilar in texture. These differences also hold for *analis*, which has, in addition, tail and rump feathers barred with white. *D. analis* and *D. atratus* overlap widely, geographically, but may be ecologically isolated. Thus some of the differences between *analis* and *macei* might have originated as species-specific recognition marks in reference to *atratus*.

Dendrocopos major

Vaurie (1959*a*) puts the race *parroti* (Hartert) from Corsica as a synonym of the Sardinian form *harterti* (Arrigoni). I prefer to recognize *parroti* as there appears to be very little overlap in bill length and the bills of all our specimens of *parroti* are noticeably more massive than those of specimens of *harterti* of the same sex. In view of the only slightly differentiated and intergrading continental races of this woodpecker that are currently recognized it seems better not to lump these two island forms.

Vaurie considers it most probable that *D. m. tianshanicus* represents inter-specific hybridization between *major* and *leucopterus*. With one exception our specimens all seem nearer to *major* and I provisionally treat them as a form of *major* and not as hybrids. The exception to this, mentioned above, is a female from the Tekkes Plain (B.M. No. 1931.7.8.259) which was originally identified as *leucopterus* and later re-identified by Vaurie as *tianshanicus*, because it had a wing measurement of 137 mm. as against 120–129 mm. for 23 females of *leucopterus* measured by Vaurie and because he considered the white spots on its wings too small for *leucopterus*. I think this bird was correctly identified originally. The very large measurement of its right wing appears to be due to the make-up of the skin. The left wing measures only 130 mm. and 11 other females of *leucopterus*, picked at random, have wing measurements ranging from 125 to 131 mm. The white spots on its wings do not appear to be significantly smaller than those of some other specimens.

PICOIDES

I agree with Delacour that this genus is very close to *Dendrocopos*. Its lack of red pigments, or rather their replacement by yellow; its flatter bill and its lack of a fourth toe are, in combination, perhaps just sufficient grounds for keeping it in a separate genus. It is certainly convenient to do so and the two *Picoïdes* species are, unquestionably, much more closely related than either is to any other.

However, although *Picoïdes* seems to have diverged a little further from the *Dendrocopos* species in the course of evolution than these have from one another it is, I think, likely that it may be phylogenetically closer to the American *Dendrocopos* species than these are to Old World forms.

The colour pattern of *Picoïdes tridactylus* is very close to that of *Dendrocopos villosus*. This is especially so with the northern Old World forms of *tridactylus*. The relatively greater amount of difference between the New World forms of *tridactylus* and *villosus* may be due to character displacement although in some other Holarctic species or superspecies there is a tendency for the New World representatives to show a greater amount of melanin pigment than the Old World forms (e.g. *Numenius phaeopus*, *Branta bernicla*). In this connection it is of interest that nominate *P. t. trydactylus* has a broad white stripe down its back like *D. villosus* whereas the American forms, e.g. *P. t. fasciatus*, show white cross-barring very like that of the "ladder-backed" *Dendrocopos* species and similar in position and extent to that of *D. stricklandi*.

The Arctic Three-toed Woodpecker *P. arcticus*, which is entirely American in distribution, has a wholely black back with, sometimes, a hint of barring indicated by white tips to one or two feathers. In the large amount of black in its plumage generally *arcticus* stands in about the same relation to American forms of *tridactylus* as these latter do to most of the Old World forms of their species. Although now largely sympatric with the smaller *tridactylus*, *arcticus* must, presumably, have evolved in isolation from *tridactylus* or proto-*tridactylus*. The very dark, and now apparently geographically isolated, Tibetan form of *tridactylus*, *P. t. funebris*, is suggestive in this connection as it shows similar, and nearly as great, contrast to the northern Old World forms of its species as does *arcticus* to American forms of *tridactylus*.

Sapheopipo noguchii

The Okinawa Woodpecker, originally included in the genus *Picus* (Seebohm, 1887), was placed by Hargitt (1890) in the monotypic genus *Sapheopipo*, which he having: "wing very long and pointed; tail only equal to the second primary and falling short of the longest by about an inch". It is found only in Okinawa, in the central Ryukyu Islands, south of Japan.

The general coloration of *noguchii* is dark olive, more or less suffused with red, especially on the tips of the feathers, on back, rump and underparts; with dark brownish-black wings and tail. It is thus, superficially, most like the dark red Sumatran form of *Picus canus*, *P. c. dedemi*. It has, however, very clear indications (see Text-fig. 9) of head and breast markings nearly identical to those of many *Dendrocopos* species and quite unlike those of any species of *Picus* or *Dinopium*. Also those parts of the primaries that are not visible, or at any rate would not be conspicuous, when the wings are closed have white markings similar to and I think homologous with those of *D. leucotos owstoni*, the very dark race of *D. leucotos* from the northern Ryukyu islands. The legs and irides of *noguchii* and *owstoni* agree in colour although their bills do not (Kuroda, 1925).

The difference of coloration between *leucotos* and *noguchii* is very similar to what one finds between many other species and their island derivatives, for example the pigeons *Columba arquatrix* and *C. pollenii*. They seem to have involved, assuming *noguchii* to be derived from *Dendrocopos* stock, simply a spread of dark pigment together with some lessening of its intensity and the spread into some of these dark areas of red or yellow pigments; or, perhaps, their revelation through their no longer being completely masked by melanin pigments. The pale colour of the bill might be similarly caused. In proportion and in the shape and structure of its bill *noguchii* is quite close to *leucotos* although its bill is proportionately longer, a common feature with island forms. Its type of sexual dimophism is identical with that of *leucotos* and several other *Dendrocopos* species. *D. leucotos owstoni* is, presumably, a more recent invader of the Ryukyu Islands that is already beginning to evolve in the same direction as has *noguchii*.

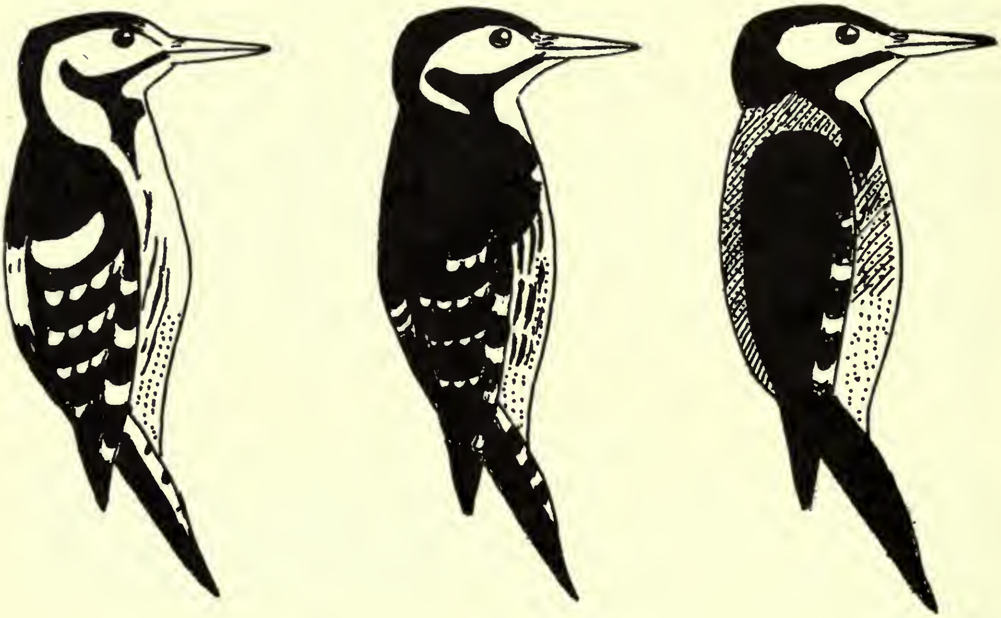

Fig. 9. Diagrammatic sketches to show resemblances and differences of colour patterns of *Dendrocopos leucotos* from northern Europe (left), same species from northern Ryu-kyu Islands (middle) and *Sapheopipo noguchii* (right).

I think that *noguchii* is an offshoot of *Dendrocopos* stock and is rather more likely to have derived from *Dendrocopos leucotos* subsequent to the speciation of the latter than from a more primitive common ancestor to them both. It is said (Kuroda, 1925) to be found on or near the ground in damp woods or bamboo jungle and never in tall trees during the day (he does not say whether it roosts in tall trees but this is, perhaps, implied). This suggests that *noguchii's* ecology may have already diverged considerably from that of typical *Dendrocopos* species and this, together with its unusual coloration, may, perhaps, justify retention of the monotypic genus *Sapheopipo*.

If, however, further studies should show that it does not differ so markedly in habits as Kuroda's notes suggest and that there are no striking anatomical differences I would be in favour of treating *Sapheopipo* as a synonym of *Dendrocopos*.

CHRYSOCOLAPTES & *DINOPIUM*

Delacour (1951) suggested that the absence of the fourth toe is not of great phylogenetic significance in woodpeckers and that in this character *Brachypternus* with its greatly reduced fourth toe, placed by Peters (1948) in the synonymy of *Dinopium*, forms a link between the three-toed *Dinopium* species and *Chrysocolaptes* with four well-developed toes. I agree with his opinion on both points; there can be no doubt that the species comprising the above genera are all closely allied. I provisionally maintain the genus *Chrysocolaptes* mainly on grounds of taxonomic convenience. This can, perhaps, be further justified by the fact that the three species involved—*lucidus*, *festivus* and *validus* seem very close to each other. All, apart from having four toes, agree in having some white on hind neck and mantle, admittedly vestigial in *lucidus*, almost identical facial markings which are, however, approaching obsolescence in *validus*, and bills that are longer and more massive than those of *Dinopium*. Except in the case of *Dinopium javanense* and *Chrysocolaptes lucidus*, wherever two species of either (or both) of these two genera overlap widely in range they show fairly striking differences of colour pattern.

The very similarly-coloured Golden-backed Three-toed Woodpecker, *D. javanense* and the Golden-backed Woodpecker *C. lucidus* are extensively sympatric and, in general, show similar geographic variation. They are most alike in western India, Burma and much of Malaysia where, except for the not very striking difference in the pattern on face and throat, colour differences between them are slight or non-existant. *C. lucidus* is, however, a larger bird with proportionately much larger bill. In other areas where they overlap the two show greater differences in coloration. On Java *lucidus* (race *strictus*) has a female with the top of the head yellow and rather obscurely spotted, and both sexes have only a tinge of red on the rump, whereas the *javanense* female has a black and white streaked crown and both sexes have a conspicuous red rump.

On Palawan *lucidus* has a very distinct race (*erythrocephalus*) in which both sexes have a red face and pink throat, with the usual dark striations rather reduced, the female has the top parts of her head a mixture of red and yellow-olive with light dull yellow spots, the individual feathers being red near the base, then olive with a yellow terminal spot. The Palawan form of *D. javanense* (*everetti*) is very distinct, having a boldy striped buffish and black face and the female a black forehead and crown and red nape. It is noteworthy, however, that, compared with other forms of *javanense*, this race shows parallel development to *lucidus* on Palawan, in having more red on the head than is usual in the species: females of other forms of *javanense* have no red on the nape and the males no red on the malar region as has *everetti*. They also agree in having the dark and light facial markings less pronounced than in most other forms of their respective species.

Chrysoclaptes lucidus

I provisionally follow Peters (1948) in his wide conception of this species because, on external characters, it is not possible to make any logical division among the many races or presumed races of *lucidus*. It is, however, quite possible that some of the island forms, especially in the Philippines, may have already reached specific level.

Like previous workers, I cannot separate specimens from South India from those from southern Malaya although the latter are, on average, a slightly lighter golden-yellow on the upperparts. There seems no alternative, therefore, but to continue to employ the name *chersonesus* for both these populations although it is likely that, in a phylogenetic sense, *chersonesus* from southern India are more closely allied to *guttacristatus* from Bengal than they are to *chersonesus* from the Malay Peninsula.

On the different Philippine islands the races (?) of *lucidus* show great variation of head colour (besides other differences). These are comparable to the differences of head colour between undoubted species of the *Chrysocolaptes-Dinopium* group elsewhere. This is no doubt due at least partly to the lack of any closely related sympatric species on most of these islands. Nominate *lucidus* from Mindanao is, perhaps rather unfortunately, a rather nondescript or intermediate form and as it has indistinct facial markings, mixed red and yellow upperparts and the top of the female's head yellowish *and* spotted it is difficult to ally it with any one, or even any one of the main groups of Philippine forms rather than another. The interesting sequence of the immature plumages of *guttacristatus* (and other races of *lucidus*?) is described in the section on juvenile plumages.

Dinopium shorii & D. javanense

The Himalayan Golden-backed Three-toed Woodpecker and *D. javanense* are very closely allied and must have derived relatively recently from a common ancestor but they appear now to overlap without interbreeding in northern Burma. There are specimens of both from Thayetmayo and the Arrakan Hills, in the British Museum. They appear to keep or even slightly to accentuate their minimal plumage differences —pale bases to the red head feathers in *shorii*, slightly different pattern of streaks on the throat—where they overlap. Admittedly hybrids between the two would be difficult to recognize. There is a slight difference of size and bill length between them and, no doubt, this correlates with differences of ecology.

Dinopium rafflesii

I concur with Peters in thinking it preferable to put the monotypic genus *Gauropicoides* (species *rafflesii*) into the synonymy of *Dinopium*. The Olive-backed Three-toed Woodpecker, *rafflesii*, seems to link *Dinopium* with *Gecinulus*, agreeing with the former in most characters but with *Gecinulus* to some extent in its softer feather texture and generally dark and rather concolorous body plumage. The wing markings are similar in both genera.

The genus *GECINULUS*

I maintain this genus for the Pale-headed Woodpecker *grantia* and the Green Bamboo Woodpecker *viridis*. These two closely allied forms differ from the green woodpeckers of the genus *Picus* in having proportionately small bills and only three toes; also in some plumage characters in which they are closer to *Dinopium*. Although rather discrete they appear, as has been mentioned above, to be linked with *Dinopium* by *rafflesii* and probably represent a link between *Picus* and the *Dinopium-Chrysocolaptes* group.

DRYOCOPUS & *PHLOEOCEASTES*

Peters (1948) placed the American species *pileatus*, *lineatus*, *erythrops* and *galeatus* in the genus *Dryocopus* together with the old world forms *martius* and *javensis*. Presumably he did this because their outer hind toes are not longer than their outer front toes (Peters, 1948, introduction, p. 6). The characters of a narrower nasal shelf and nostrils nearer the culmen, which he says are correlated with the shorter outer hind toe, do not appear to be valid as there is much variation between species; on these characters *lineatus*, at least, seems to fit better with those species which have a longer outer hind toe. I do not think this relative length of the outer hind toe is,

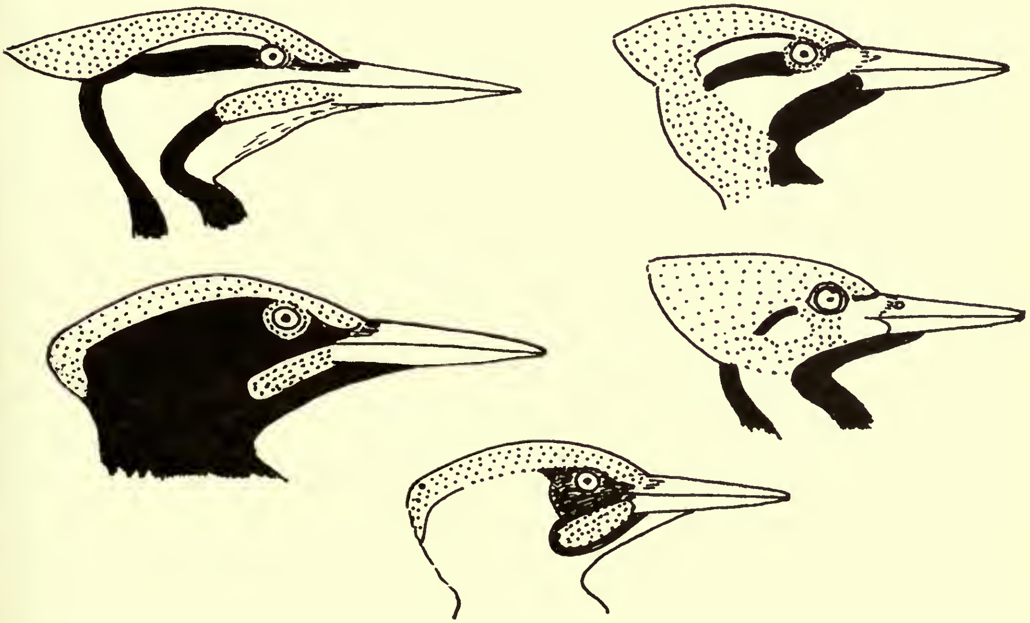

FIG. 10. Diagrammatic sketches to show colour patterns of heads of *Phloeoceastes lineatus* (top left), *Dryocopus javensis* (bottom left), *Picus viridis* (bottom middle), *Phloeoceastes* haematogaster (top right) and *P. melanoleucos* (bottom right).

by itself, a very important character. Their distribution and their plumage characters, especially the colour patterns of their heads all suggest that the American species placed by Peters in *Dryocopus* are closer to the species included by him in the genus *Phloeoceastes* than they are to Old World forms. I therefore think it best to place them in *Phloeoceastes* and restrict *Dryocopus* to the two Old World species *martius* and *javensis*.

I think it possible that *Dryocopus*, as above restricted, might prove to be more closely related to other Old World genera, such as *Mulleripicus* and *Picus*. Kilham (1959) was impressed by the great similarity between some of the behaviour patterns he had observed in *pileatus* and some described for *martius* (Blume, 1956) but comparisons of these two with both (other) *Phloeoceastes* species and *Mulleripicus* are needed. Most of sketches and descriptions in Blume's comparative study of European woodpeckers (Blume, 1961) suggest to me that the displays, and possibly even the calls, of *martius* bear a more close resemblance to those of *Picus viridis* than to those described for *pileatus* by Kilham.

Phloeoceastes divides readily into the *lineatus* species-group comprising *lineatus* (syn. *erythrops*), *pileatus*, *schulzi* and *galeatus*, all of which have rather softer, denser plumage with consequently longer nuchal crests and tend to have proportionately smaller bills, and the *melanoleucos* species-group, comprising *melanoleucos*, *guatemalensis*, *pollens*, *haematogaster*, *rubricollis*, *robustus* and *leucopogon*.

Within the *lineatus* group *pileatus*, *lineatus* and *schulzi* are closer to each other in colour patterns than any of them is to *galeatus*. This may give a false impression, as the very differently coloured (largely buffish brown) head and underwing of *galeatus* may be the result of selection for species-specific markings in reference to *lineatus* which it overlaps widely in range. *P. pileatus* does not overlap any congener and *schulzi* would appear to have only a marginal overlap with *galeatus* and *lineatus* at the northern edge of its range. Both *pileatus* and *schulzi* have concolorous black underparts unlike any other close relatives. This might, however, be due to some environmental factor as these two are in predominently temperate climates north and south, respectively, of the ranges of other *Phloeoceastes* species.

The species in the *melanoleucos* group all appear to be very closely related to each other. Within this group it is possible that relatively greater differences in colour pattern between any two species may not indicate comparable phylogenetic disparity as such differences may have evolved as isolating mechanisms in reference to each other. Although all species show differences in colour pattern these are, on the whole, most marked, and often correlated with differences of body proportions, in species that overlap widely in range. It is notable that both this and the *lineatus* group have evolved some forms predominantly white and others predominantly buff or chestnut on the under wing.

I follow Peters in thinking it best to give specific rank to both *guatemalensis* and *melanoleucos*, although they can certainly be considered as members of a superspecies. Further studies may, however, show that they are in fact conspecific and if so the rather striking differences in colour patterns of their heads may be a case of character displacement as *melanoleucos* overlaps in range with *robustus* whose male has an almost entirely red head like that of *guatemalensis*.

Pholeoceastes lineatus & *P. erythrops*

Peters (1948) says that it has been suggested that *erythrops* is a subspecies of the Lineated Woodpecker *lineatus* but that, if specimens have been correctly identified, they overlap over a wide area. He treats *erythrops* as a good species but remarks that " The inter-relationships of the *lineatus-erythrops-schulzi* group are quite involved and require additional field study ".

Van Rossem (1934) and De Schauensee (1966) have both presented evidence that *erythrops* and *lineatus* are conspecific. I have compared specimens of both from Sapucay, Paraguay and they differ in no character except the presence (in *lineatus*) or absence (in *erythrops*) of white on the scapular region. Van Rossem states that some specimens of *erythrops* show white markings on the shoulder region and one of our specimens has one white-edged feather in this region. I think the evidence suggests that *lineatus* is dimorphic over the southern-most part of its range and that *erythrops* is merely a black-shouldered morph of this species.

CAMPEPHILUS & IPOCRANTOR

Hargitt (1890) followed Cabanis & Heine (1863) in placing the Magellan Woodpecker in the monotypic genus *Ipocrantor*; Peters (1948) placed it with the ivory-billed woodpeckers in the genus *Campephilus*. Peters was, presumably, led to this because its rather large size (in comparison with *Phloeoceastes* species), soft, glossy black plumage, large white wing patches and the long crest of the female combine to give it a very similar general appearance to an ivory-bill. Although it is possible that *magellanicus* does represent a divergence from the same stock as produced the ivory-bills, subsequent to the latter's splitting off from ancestral *Phloeoceastes*, I think this rather unlikely.

The coloration and colour-patterns of the heads of both *magellanicus* and the ivory-bills are closer to those of *Phloeoceastes* than they are to each other. In both *magellanicus* and the ivory-bills the colour pattern of the head seems to represent a modification and some degree (considerable in *magellanicus*) of simplification of a pattern typical of *Phloeoceastes*. This simplification has involved a reduction in the amount of red in the male ivory-bills and its increase in the male of *magellanicus*. The white wing patch of *magellanicus* might represent a restricted version of that found in the ivory-bills but could equally (in both) be a development from the white or light bars that some *Phloeoceastes* species show on (some of) the inner webs of the primaries and secondaries. The under wing pattern of *magellanicus* is closer to that of *Phloeoceastes melanoleucos* and *P. guatemalensis* than it is to that of *Campephilus*. The bill of *magellanicus* is dark, not white or cream-coloured. Some species of *Phloeoceastes* have pale bills (others have dark bills).

It is, I think, likely that the features in which *magellanicus* agrees more closely with the ivory-bills than it does with *Phloeoceastes* species: length of crest of female, relatively lax, glossy plumage and rather long tail (all, probably, correlated characters) are due to convergence in related stocks but that each is, phylogenetically, at least as closely related to *Phloeoceastes* as to the other. I think, therefore, that it is preferable to retain the monotypic genus *Ipocrantor* for *magellanicus*. The only reasonable alternative, and one that seems to have much to recommend it, would be to place all these large, related, predominantly black, white and red woodpeckers in the single genus *Campephilus*. I feel, however, that it would be premature for me to do so now in view of the work currently being done in the U.S.A. on the habits and ecologies of the American woodpeckers which will, doubtless, soon provide other and perhaps firmer grounds for taking or refraining from this course.

Variant individuals

The commonest plumage variation in woodpeckers, occurring in individuals of many green-backed and golden-backed species, is for the green or golden parts of the plumage, especially on the mantle, to be more or less suffused or mottled, with red. This correlates with the existence of several red-backed forms closely related to or even conspecific with green-backed and golden-backed forms. Other variants in the British Museum (Nat. Hist.) collection are listed and described below.

Picus vittatus

A male from Pulau Langkawi, Malay Peninsula (B.M. No. 1936.4.12.586) shows an apparent reduction of red and yellow pigments. Its breast, underparts and sides of face are paler and more buffy than in normal specimens. The green of its upperparts is a colder hue, less tinged with yellow, and the red parts of its head a light flame-orange instead of the deep scarlet-crimson of normal birds.

Dendrocopos assimilis

A male from Khipri, Sind (B.M. No.1898.12.12.331) has the red on the head replaced by straw yellow except for the nuchal region and a line extending thence above each eye, where it is orange-red, not the normal dark scarlet.

Dendrocopos himalayensis

A supposed male from near Simla (B.M. No.1887.8.10.7) has the belly, flanks and much of the lower breast red, instead of this colour being confined to the under tail coverts and post-cloacal area as in normal specimens. Surprisingly, if it is correctly sexed, it shows much less red on the head than normal, this being confined to the tips of only about a third of the crown feathers. It would seem strange if the bird exhibited an excess of red pigment in one area yet a decrease of it elsewhere and I am inclined to think that it may be a female, in which case (the female having normally no red on the head) its head coloration would, like that of its underparts, represent an increase of red.

Dendrocopos syriacus

An adult female (B.M. No.1888.11.1.564) shows partial albinism. It has many white or partially white feathers on normally black areas of head, back and wings. The distribution of red is normal.

Dendrocopos atratus

A presumed female from the Southern Shan States of Burma (B.M. No.1903.12.24.53) shows an interesting coloration as a result of partial loss of melanin pigment. It gives a general impression of having most of the normally black areas replaced with light grey. More closely examined it shows, on its upperparts, a narrow edging of more intensely pigmented (darkish grey) plumage posterior to every white marking (except where this comes to the end of the feather) and a similar but broader dark edge immediately anterior to it. This is most clearly seen on the secondaries but holds good for all other feathers. On the outer webs of the outer primaries the dark grey areas are more extensive. The tail shows ill-defined light and darker grey transverse barring but the modified, supporting, central feathers have their tips and the edges of both webs more heavily pigmented, a dark brownish grey. The top of the head is noticeably darker than most of the back, being, at least so far as the tips of most feathers are concerned, a very brownish grey, almost blackish. Due, presumably, to the reduction of melanin the underparts look much paler and more yellowish than normal, the dark streaks are greyish brown, not brownish black, and the red under tail coverts lighter and brighter.

It would be interesting to know whether the areas (tail tips, primary edges] etc.) which show stronger pigmentation in this individual also have in fact more melann in normal birds where it is not visually evident. As they all seem to be areas that are likely to need " extra " strengthening, this would seem probable.

Dinopium benghalense

A male from southern Konkan (B.M. No.1887.8.10.1957) and a male from Khandeish (B.M. No.1880.1.1.225) both have many red-tipped feathers in the malar region, giving much the impression of the type of black-enclosed red malar stripe found in males of *Picus viridis*. Normally *D. benghalense* has no red in the malar region in any plumage phase.

A female from Sind (B.M. No.1941.5.30.1391) shows reduction of red and yellow pigments. The normally golden parts of the mantle are a pale straw yellow, the normally scarlet nuchal crest more or less cream, intermixed with some partially orange-pink feathers.

A female from Lucknow (B.M. No.1887.8.10.1932) although normal in coloration, seems worth mentioning here. It has an abnormally long bill with decurved culmen which looks more like a Hoopoe's bill than a woodpecker's. The culmen measures 64 mm., as against 36 to 38 in normal females, and overlaps the under mandible by 7 mm. The bill tips are narrow and flexible and it is impossible to believe that the bill could have been used at all for wood-pecking. The bird had evidently been able to obtain food as is adult and in good plumage.

Phloeoceastes lineatus

Male from eastern Ecuador in post-juvenal moult (B.M. No.1940.12.5.93). Has the central part of the crown and nuchal region bright straw yellow, tinged orange, instead of red. The red on the forehead and sides of head is a little lighter in hue than usual.

Dinopium javanense

Three females of the race *intermedium* show some trace of red in the head plumage. No. 1921.12.31.92, from western Siam has several male-type red feathers, two of them long nuchal feathers, on the left side of its head. No. 1927.6.5.419, from Tonkin, has one red-tipped but otherwise female-type feather above its left eye and No. 1927.6.5.1587, from Cochin-China, has several red-tipped but otherwise sexually intermediate-looking feathers.

Many of the above variants involve partial loss of pigmentation and are comparable in appearance, and probably in origin, to relatively common varieties in other groups. It is, however, of interest that where this involves only the partial substitution of red by yellow, as in the *Dendrocopos assimilis* and the *Phloeoceastes lineatus*, it is comparable to one of the more conspicuous differences in coloration often found between related species of woodpeckers. This, of course, is also true of the second type of variant included above, where individuals show red on areas not normally so-coloured in their sex or species.

SUMMARY

Some aspects of taxonomy and relationships of the woodpeckers are described and discussed. Certain close resemblances in coloration and ecology are due to convergence. In all geographic regions inhabited by woodpeckers the smallest species are about the same size; the same is true for the largest species except that there are no large arboreal species in the Ethiopian region. The typical forms of sexual dimorphism and the exceptions to them are described.

Juvenile woodpeckers usually have bright pigments similar to, but not always identical with, those of the adults. When all species are considered, the juveniles approximate more closely to the family average in the amount of red or yellow on the head than do the adults. In no instance, however, is the juvenile plumage considered to be more conspicuous than the adult male's.

Leuconerpes is treated as a synonym of *Melanerpes*. The species *obsoletus* is considered to be referable to *Dendropicos* not *Dendrocopos*. *Geocolaptes* is related to other African genera, not to *Colaptes*. It is thought that all the New World species of *Dendrocopos* are more closely related to each other than any one of them is to any Old World species. *Sapheopipo* is a recent derivative of *Dendrocopos*. Some of the Philippine Island races of *Chrysocolaptes lucidus* show colour differences comparable to those shown by different species of the *Chrysocolaptes-Dinopium* group elsewhere. The New World forms currently placed in *Dryocopus* seem better placed in *Phloeoceastes*. Unless all the large black, white and red American woodpeckers are to be treated as congeneric, it is best to retain the monotypic genus *Ipocrantor* for the species *magellanicus*.

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BY

R. ETHERIDGE

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Pp. 45–64 : 2 *Text-figures*

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A REVIEW OF THE IGUANID LIZARD GENERA *URACENTRON* AND *STROBILURUS*

By RICHARD ETHERIDGE

SYNOPSIS

The external morphology, distribution, and systematics of the iguanid lizard genera *Uracentron* and *Strobilurus* are reviewed. Four species of *Uracentron* and one species of *Strobilurus* are recognized, and a key is given to the species of *Uracentron*. Two species erroneously referred to *Uracentron* are discussed.

INTRODUCTION

Uracentron and *Strobilurus* are South American iguanid lizards belonging to a group of genera that I have called the " tropidurines ", (Etheridge, 1964 : 629). Within this group *Uracentron* is easily identified by its very large interparietal scale, and short, spiny tail, and by the absence of a row of scales aligned mid-dorsally. *Strobilurus* is closely allied to it, and like *Uracentron* has a very large interparietal scale and a spiny tail ; it differs in having a row of scales aligned middorsally. Also, the tail of *Uracentron* is flat, nonautotomic, and scarcely more than half as long as the head and body, whereas the tail of *Strobilurus* is nearly cylindrical, autotomic, and about as long as the head and body.

Of the species we now know under the genus *Uracentron* the first was described as *Lacerta azurea* by Linnaeus (1758 : 202). Prior to this the species had been figured by Seba (1734 : 2 : 62 : 6), and Linnaeus (1754 : 42) had described in some detail specimens then in the Museum of King Adolf Fredrik of Sweden. *Lacerta azurea* was subsequently combined with diverse other lizards that also have a spiny tail under the genera *Stellio* (Latreille, 1802 : 29 and 34 ; Daudin, 1802 : 36 and 40 ; Fitzinger, 1826 : 49), and *Uromastyx* (Merrem, 1820 : 56–7). The generic name *Uracentron* was introduced by Kaup (1826 : 88), and in the following year he included *Uracentron* in his list of the New World lizards (Kaup, 1827 : 612). The latter publication was cited as the original description of the genus by Burt & Burt (1933 : 48). Wagler (1830 : 145) changed the spelling to *Urocentron*, and with few exceptions (Mertens, 1925 : 75 ; Dunn, 1944 : 89 ; Valdivieso & Tamsitt, 1963 : 31 ; Peters, 1967 : 36) all later authors either adopted the change, or altered it still again to *Uranocentron* (Gray, 1831 : 42, 1845 : 225; O'Shaughnessy, 1881 : 245), or to *Urocentrum* (Boulenger, 1894 : 729; Werner, 1900 : 4). Cuvier (1829 : 34) proposed *Doryphorus* as a substitute name, and for a time it was also in use (Schinz, 1835 : 92 ; Guérin-Méneville, 1829–1838 : 8 ; Duméril & Bibron, 1837 : 369 ; Guichenot, 1855 : 26 ; Duméril, 1856 : 559 ; Cope, 1870 : 556).

Boulenger (1885 : 182–184) recognized three species of *Uracentron : azureum* (Linnaeus, 1758), *flaviceps* (Guichenot, 1855), and *castor* (Cope, 1870), and later he described a fourth species, *U. guentheri* (Boulenger, 1894 : 729). A fifth species was described by Mertens (1925 : 75), *U. werneri*. Burt & Burt (1933 : 48–9) recognized five species of *Uracentron* in their Checklist of South American Lizards. They included *U. meyeri* (Werner, 1900 : 4), and *U. palluma* (Tschudi, 1845 : 35), neither of which is correctly referred to the genus *Uracentron*, and they failed to include *U. flaviceps* and *U. werneri*.

In the present study *U. meyeri* and *U. palluma* are removed from the genus *Uracentron*, *U. castor* is placed in the synonymy of *U. flaviceps*, and this species together with *U. azureum*, *U. guentheri*, and *U. werneri* are considered valid species.

Strobilurus is, and has always been, considered monotypic, with the single species *S. torquatus* (Wiegmann, 1834 : 18).

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During the course of this study I have had the good fortune to work in a number of museums in Europe and in the United States. I should like to express my appreciation to those curators who have allowed me to examine the collections in their care : Mr. C. M. Bogert, the American Museum of Natural History, New York ; Dr. E. E. Williams, the Museum of Comparative Zoology, Harvard ; Dr. R. F. Inger, the Field Museum of Natural History, Chicago ; Dr. A. Leviton, the California Academy of Sciences ; Dr. J. A. Dixon, the Los Angeles County Museum ; Miss A. G. C. Grandison, British Museum (Natural History), London ; Monsieur J. Guibé, Muséum National d'Histoire Naturelle, Paris; Dr. K. Klemmer, Natur-Museum und Forschungs-Institut Senckenberg, Frankfurt ; Dr. J. Eiselt, Naturhistorischen Museum, Vienna ; Dr. C. Edelstam, Naturhistoriska Riksmuseet, Stockholm ; Dr. H. Wermuth, Staatliches Museum für Naturkunde, Ludwigsburg ; Dr. J. A. Peters, United States National Museum, Washington ; Dr. G. Peters, Institut für Spezielle Zoologie und Zoologisches Museum der Humbolt Universität, Berlin ; Dr. W. Ladiges, Zoologisches Staatsinstitut und Zoologisches Museum, Hamburg ; Dr. F. W. Braestrup, Zoologiske Museum, København ; Dr. W. Hellmich, Zoologisches Sammlung des Bayerischen Staates, Munich. I should also like to thank Mr. E. V. Malnate, Academy of Natural Sciences of Philadelphia, for providing me with information on the holotype of *U. castor*.

I am especially grateful to Miss A. G. C. Grandison and her staff at the British Museum (Natural History) where most of this work, including the preparation of this manuscript, was undertaken.

The following abbreviations are used :

A.M.N.H.	American Museum of Natural History, New York.
A.N.S.P.	Academy of Natural Sciences of Philadelphia.
B.M.N.H.	British Museum (Natural History), London.
C.A.S.	California Academy of Sciences, San Francisco.
F.M.N.H.	Field Museum of Natural History, Chicago.
L.A.C.M.	Los Angeles County Museum, Los Angeles.
M.C.Z.	Museum of Comparative Zoology, Harvard University, Cambridge.
M.H.N.P.	Muséum National d'Histoire Naturelle, Paris.
N.M.W.	Naturhistorischen Museum, Wien (Vienna).
N.R.M.S.	Naturhistoriska Riksmuseet, Stockholm.
S.M.F.	Natur-Museum und Forschungs-Institut Senckenberg, Frankfurt.

S.M.N.L.	Staatliches Museum für Naturkunde, Ludwigsburg.
U.S.N.M.	United States National Museum, Washington.
Z.M.B.	Zoologisches Museum der Humboldt Universität, Berlin.
Z.M.H.	Zoologisches Staatsinstitut und Zoologisches Museum, Hamburg.
Z.M.K.	Zoologiske Museum, København (Copenhagen).
Z.S.B.S.	Zoologisches Sammlung des Bayerischen Staates, München.

URACENTRON Kaup, 1826, Isis (von Oken), 19 : 88.

Type species *Lacerta azurea* Linnaeus.

Diagnosis. *Uracentron* belongs to that group of South American-West Indian iguanids that is distinguished by the presence of a large sternal fontanelle and the absence of femoral pores, the " tropidurines " (Etheridge, 1964 : 629). Within the tropidurines *Uracentron* is probably most closely allied to *Strobilurus*, *Tropidurus*, *Plica*, and *Platynotus*, all of which have a very large interparietal scale. *Uracentron* differs from these genera in having a short, spiny, nonautotomic tail that is about one half as long as the head and body ; in the others the tail is at least as long as the head and body, and is autotomic. Among South American iguanids only the unrelated *Hoplocercus* has a tail similar to *Uracentron*'s, but *Hoplocercus* may be easily distinguished by its small interparietal and heterogeneous dorsal squamation.

Characteristics. Upper head scales polygonal, juxtaposed, slightly to moderately convex, with a distinctly granular surface. Supraorbital semicircles poorly differentiated ; scales in frontal and prefrontal regions similar to other snout scales. Three or four pair of frontals, of which one to three may be in contact medially between the orbits, or separated by a median row of small scales. One to three rows of enlarged supraoculars, at least some of which are transversely expanded. Enlarged supraoculars usually separated from frontals and frontoparietals by two rows of small scales. Interparietal scale very large, one third to one fourth as wide as the head, narrower in front, usually longer than wide, with a central " eye ". Nasal large, dorsal, separated from rostral and upper labials by a row of scales ; opening large, directed dorsally in the posterior part of the scale. One or two large, convex, overlapping canthals. Canthals followed by six elongate superciliaries, each overlapping the one behind, followed by three shorter scales that overlap in the opposite direction. Two or three large scales in loreal region. A wide, elongate subocular scale with a keel along its upper margin, preceded by two or three shorter but similar scales that border the orbit anteriorly. A single row of rather large loreolabials, ending below the subocular, which posteriorly forms a short suture with the last upper labial. Upper labials large, more or less rectangular. Temporals polygonal, juxtaposed, smooth or keeled. Lower labials similar to upper labials but larger still. No enlarged postmental scales. Gulars small, mostly hexagonal, convex, juxtaposed or subimbricate, reduced in front of the anterior transverse gular fold, enlarged and imbricate in front of the posterior transverse gular fold. Tympanum about as large as the eye, without projecting scales along its anterior margin.

No scale row aligned mid-dorsally. Dorsal and lateral scales of neck and anterior body small, convex and juxtaposed, or keeled and imbricate. Remaining dorsal and lateral scales of body larger, imbricate, smooth or keeled. Ventral body scales imbricate, smooth or faintly keeled, larger than dorsals.

Tail short, not autotomic, about one half as long as the head and body, moderately or strongly depressed, with equal whorls of large, spinose scales.

Limbs covered with rhomboidal, imbricate scales, smooth or keeled, those on the posterior surface of the thighs reduced. Scales of palms and soles imbricate, denticulate, smooth or faintly keeled. Subdigital lamellae mostly tricarinate and tridenticulate, the keels becoming faint on the distal lamellae.

Two transverse gular folds present, the anterior one just posterior to a line even with the lower border of the tympanum, and with normal gular scales ; the posteror fold formed by ventromedial extensions of the antibrachial folds, and enclosing reduced but not granular scales. Antibrachial folds extend up and back over the forelimbs, then slant back and downward along the side of the body, fading out about midway to the hind limbs. Sides of neck with well developed, irregular folds. A ventrolateral longitudinal fold present between the forelimb and hind limb insertions.

Scales on top and sides of head and on chin with numerous, closely set scale organs. Body scales with a single scale organ or none at all. Caudal scales with several prominent scale organs along posterior edge on each side of keel. No femoral or preanal pores.

Uracentron azureum (Linnaeus)

Lacerta azurea Linnaeus, 1758, p. 202 (type locality, Africa; here restricted to the vicinity of Paramaribo, Surinam).
Stellio brevicaudata Latreille, 1802, p. 29 (type locality, interior of Guiana and Surinam).
Stellio azureus Latreille, 1802, p. 34.
Stellio brevicaudatus Daudin, 1802, p. 40.
Stellio azureus Daudin, 1802, p. 36.
Uromastyx caeruleus Merrem, 1820, p. 56 (substitute name for *Stellio azureus*).
Uromastyx azureus Merrem, 1820, p. 57.
Uracentron azureum Kaup, 1826, c. 88.
Uracentron coeruleus Kaup, 1826, c. 88.
Doryphorus brevicaudatus Cuvier, 1829, p. 34.
Doryphorus azureus Cuvier, 1829, p. 34.
Urocentron azurea Wagler, 1830, p. 45.
Ophessa (*Uranocentron*) *brevicaudatus* Gray, 1831, p. 42.
Ophessa (*Uranocentron*) *azureus* Gray, 1831, p. 42.
Urocentron brevicaudatum Wiegmann, 1834, p. 48.
Urocentron azureum Fitzinger, 1843, p. 77.
Urocentron azureum Boulenger, 1885, p. 182.

SYNTYPES. No. KaF 1900 : 113 (2 exs) in the Naturhistoriska Riksmuseet, Stockholm, Sweden.

TYPE LOCALITY. In listing Africa as the type locality of *Lacerta azurea*, Linnaeus (1758 : 202) probably was misled by Seba (1734 : 2 : 62 : 6), who had figured this species and given Africa as its origin. Nevertheless, Linnaeus did have before him two specimens upon which his description was based, and there is reasonably good evidence that they had come from the neighbourhood of Paramaribo, Surinam.

Many of the species of South American plants and animals described by Linnaeus were collected by Carl Gustaf Dahlberg, a man of Swedish nationality, who arrived in Surinam in 1746, where he acquired plantations on Peruca Creek, and Cottica River, within 100 km of Paramaribo. In 1754, during one of his return trips to Sweden, Dahlberg presented his collections to King Adolf Fredrik and in the same year Linnaeus (1754 : 42) described specimens of *Lacerta azurea* in the museum of the King. When Dahlberg returned to Surinam in 1755 he took with him Daniel Rolander at the request of Linnaeus, who at least partly financed Rolander's trip. Rolander was a former student of Linnaeus, and private tutor to his son. Rolander is known to have collected in the neighbourhood of Paramaribo, and also went up the Commewijne River. The unrest caused by the revolt of escaped negro slaves prevented him from penetrating deeper into the interior of Surinam, and in 1756 he returned to Sweden. Part of Rolander's collection was purchased by the Swedish Baron de Greer, who in turn presented the specimens to Linnaeus (Holthuis, 1959 : 17–21).

Most of the South American species of lizards described by Linnaeus, including *Uracentron azureum*, are widely distributed in the northern part of the continent, and are known to occur at Paramaribo. It seems probable that many, if not all, of Linnaeus' specimens were from the collections of Dahlberg and Rolander, made in the vicinity of Paramaribo. I therefore propose the restriction of the type locality of *Uracentron azureum* to the vicinity of Paramaribo, Surinam.

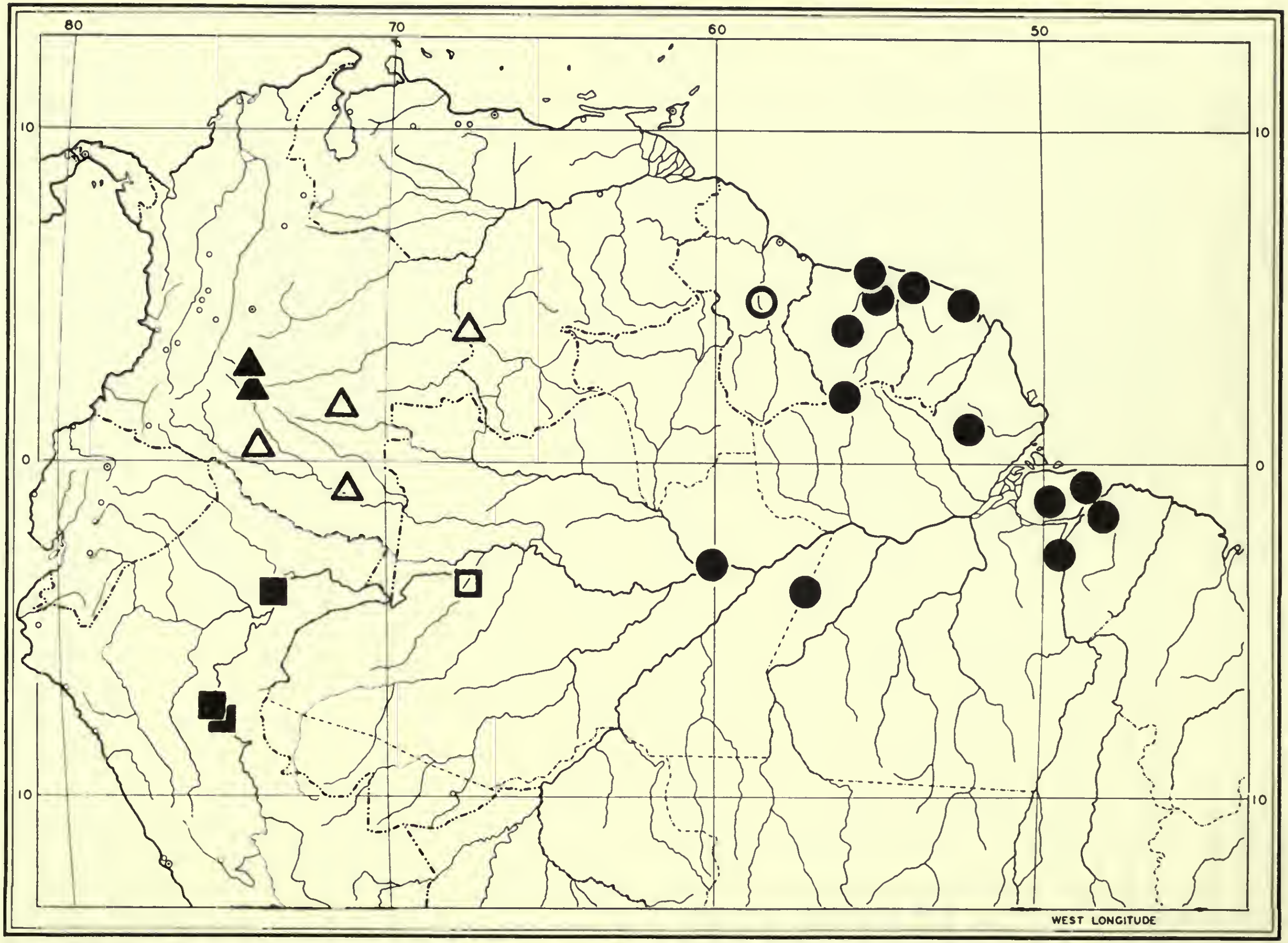
CHARACTERISTICS. The supraoculars are variable in shape ; one, two, or two and a half rows of enlarged scales may be present. The scales of the inner row are always to some extent transversely widened, but never strap-like. The enlarged supraoculars are always separated from the superciliaries by two rows of small scales.

The dorsal and lateral scales of the neck and anterior part of the body are very small, smooth, convex, and juxtaposed. Posteriorly the dorsal and lateral scales of the body become larger, imbricate, and obtusely keeled, largest in the sacrolumbar region. The ventral scales are smooth. Scale counts are given in Table I.

The tail is moderately depressed, with about 21 whorls of large, spinose scales. A whorl halfway between the vent and the tip of the tail contains about 13 scales. The tail is 0.48 to 0.65 (mean, 0.58) times as long as the head and body.

The snout-vent length of the largest male examined is 87 mm, of the largest female 86 mm.

Colour in preservative : the upper surfaces are bluish-grey, with bold, black markings. The medial half of the supraocular region is black, and there is usually a median, V-shaped mark in front of the frontal region. A W-shaped mark on the back of the head has its median apex on the interparietal scale, and its horns extend down to the suboculars. Two crescentric bands cross the neck, the extremities of the anterior one curving down through the tympani to the angle of the mouth.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WEST LONGITUDE

FIG. 1. Map of northern South America showing localities for *Uracentron azureum* (circles), *U. guentheri* (squares), and *U. werneri* (triangles). Inexact localities are indicated by open symbols.

A series of similar crescentric bands cross the back, the extremities of the first curving down into the antihumeral folds. Five or six bands may be present between the shoulders and the sacrum, or the posterior one, two, or three bands may be broken and off-set at the dorsal midline, or may be broken up into a bold reticulum. A black reticulum covers the upper surfaces of the limbs, and is most intense on the hind limbs. The tail has irregular black marks above, and about one half of the spines along the sides of the tail are tipped with yellow. Below, the throat is dark bluish-grey. The belly is a lighter grey, and the ventral surface of the tail is dark bluish-grey along the sides, with a yellowish area down the middle.

Mr. Marinus S. Hoogmoed has furnished me with colour notes on a living individual captured along Feticreek, Litani River, in Surinam. The colour is described as " head and back yellow-green mottled, tail with yellow points, throat yellow-green ; belly, underside of legs grey-blue ". Cott (1926) has published an excellent coloured illustration of this species.

RANGE. (Text-fig. 1). Records of *Uracentron azureum* are from British Guiana, French Guiana, and Surinam, and from along, or near the Amazon River in north-eastern Brazil, as far west as Manaus. *U. azureum* and *U. flaviceps* occur together at Manaus.

MATERIAL EXAMINED. *British Guiana* : no specific locality B.M.N.H. 1905.10.21.1. *Surinam* : Bergenaal N.M.W. 13926 (2 exs) ; no specific locality. M.H.N.P. 2515, Z.S.B.S. 534/0, M.C.Z. 4500. *French Guiana* : Cayenne M.H.N.P. 196, 2514, 2396 ; Saint Laurent M.H.N.P. 24.121 ; Mornes du bas Mahurg M.H.N.P. 03.20 ; no specific locality M.H.N.P. 8211, 2516, B.M.N.H. 1920.1.20.1334, Z.S.B.S. 534/0. *Brazil* : Amazonas, Manuas B.M.N.H. 1922.6.15.1, C.A.S. 84247 ; Amazonas, Manjuru River A.M.N.H. 101945 ; Pará, Ilha Marajó, Soute S.M.F. 24930 ; Pará, Ilha Marajó, Dist. Calderão Z.S.B.S. 37/1924 (5 exs), Z.M.H. 4421 (5 exs), 4496 ; Pará, Ilha Marajó B.M.N.H. 1923.11.9.68–72, 1926.5.5.5, S.M.F. 24931 ; Pará, within 50 miles of Belem M.C.Z. 53216 ; Pará, Amnuathena, Rio Tocantíns Z.S.B.S. 674/1920 ; Amapá, Serra do Navio S.M.F. 59580 ; Maranhão S.M.F. 11202 ; no specific locality M.H.N.P. 92.290, 99.215, N.M.W. 13928.1, B.M.N.H. 51.7.17.45, A.M.N.H. 58277–9, 60330–2. South America : no specific locality B.M.N.H. 47.2.19.6, 59.12.28.2, 66.8.14.302, N.M.W. 13927 (2 exs), N.R.M.S. Kaf 1900 : 113 (syntypes), S.M.N.L. unnumbered.

Additional records from Surinam have been provided to me (*in litt.*)by Mr. Marinus S. Hoogmoed : Litani Fetikreek, Sipaliwini, Paloemeu, Berg en Dal, and Moengo.

Uracentron guentheri Boulenger

Urocentrum guentheri Boulenger, 1894, p. 729 (type locality : Iquitos, Peru).
Urocentron guentheri Burt and Burt, 1933, p. 49.

HOLOTYPE. No. 93.7.10.13 (RR 1946.8.29.85) in the British Museum (Natural History), London. Collector, A. E. Pratt.

CHARACTERISTICS. Four or five transversely widened, band-like supraocular scales are present in a single row, all in contact laterally with the superciliaries, or the first two or three may be separated from the superciliaries by a row of very small scales.

The dorsal and lateral scales of the neck and anterior part of the body are very small, smooth, convex, and juxtaposed. Posteriorly the dorsal and lateral scales of the body become larger, imbricate, and weakly, obtusely keeled, largest in the sacrolumbar region. The ventral scales are smooth. Scale counts are given in Table I.

The tail is moderately depressed, with about 21 whorls of large, spinose scales. A whorl halfway between the vent and the tip of the tail contains about 13 scales. The tail is 0.52 to 0.57 (mean 0.54) times as long as the head and body.

The snout-vent length of the largest male examined is 75 mm., of the largest female 75 mm.

Colour in preservative : the upper surfaces are bluish-grey with black markings. Many of the head scale sutures are edged in black, and the supraocular region on each side is outlined in black, with a black bar across the middle. On the frontals is a median, longitudinal black bar. Five or six narrow, somewhat irregular, crescentric bands cross the posterior part of the head and neck, with the horns of each crescent pointing downward and forward. Across the shoulders is a similar, narrow crescent that descends on each side into the antihumeral folds. The upper surface of the limbs and most of the back are covered by a bold reticulum of black lines. In the middle of the anterior part of the back the reticulum tends to form short, transverse bars. On the hind leg the reticulum extends onto the posterior surface of the thigh. The caudal scales and the ends of their spines are outlined in yellow. The ventral surface of the head and body is light bluish-grey, becoming yellowish in the preanal area and under the tail. There are no records of the colour in life of this species, but is seems probable that the bluish-grey background of preserved animals is green in life. A black-and-white illustration of the pattern may be found in Boulenger, 1894 : pl. 47, fig. 3.

RANGE. (Text-fig. 1). Records of *Uracentron guentheri* are from the Río Ucayali system in the Department of Loreto in eastern Peru, and from the western Amazonian basin in northwestern Brazil. The range of *U. guentheri* apparently overlaps that of *U. flaviceps* in eastern Peru and Brazil, and the two are definitely known to occur together at Iquitos, Peru.

REMARKS. Boulenger (1894 : pl. 47, fig. 3) shows the tip of the tail of the holotype of *Uracentron guentheri* blunt. Mertens (1925 : 76) used this as a character to distinguish it from *U. werneri*. However, the blunt tail of the holotype of *U. guentheri* is due to injury; the tip is missing and the end of the tail is healed over with scar tissue. The tail has 16½ rows of spinose scales ; about 5½ rows are missing.

MATERIAL EXAMINED. *Peru* : Dept. Loreto, lower Río Cushdbatay A.M.N.H. 56410 ; Dept. Loreto, Roaboya, Río Ucayali A.M.N.H. 57204 ; Dept. Loreto, Rian Rian, Contamana region, Río Sahnaya Valley A.M.N.H. 57205 ; Dept. Loreto, Iquitos B.M.N.H. 93.7.10.3 (RR 1946.8.29.85) (Holotype). *Brazil* : Amazonas, Río Jutai Z.M.B. 30974 ; Amazonas, Río Solimoes, Lago Calado S.M.F. 30304/5.2.

Uracentron werneri Mertens

Uracentron werneri Mertens, 1925, p. 75 (type locality : upper Orinoco, Venezuela).

HOLOTYPE. No. 11203 in the Natur-Museums und Forschungs-Institutes, Frankfurt am Main. Collector, G. Hübner.

CHARACTERISTICS. The shape and size of the supraoculars are variable ; two or two and a half rows of enlarged scales with four or five scales in each, those of the inner row somewhat transversely widened, and those of the outer row separated from the superciliaries by two rows of small scales.

The dorsal and lateral scales of the neck and anterior part of the body are very small, smooth, convex, and juxtaposed. Posteriorly the dorsal and lateral scales of the body become larger, imbricate, and remain smooth. The ventral scales are smooth. Scale counts are given in Table I.

The tail is moderately depressed, with about 21 whorls of large, spinose scales. A whorl halfway between the vent and the tip of the tail contains about 13 scales. The tail is 0·56 to 0·60 (mean, 0·57) times as long as the head and body.

The largest male examined is 60 mm. snout-vent length, the largest female is 58 mm.

Colour in preservative : all upper surfaces are dark greyish-brown or bluish-black, somewhat lighter on the snout and sides of the head. A pattern of light spots and a dark nuchal collar is very faintly indicated in some specimens, including the holotype. The holotype has a bold, yellowish, asymetrical spot on the top of the head that covers the interparietal and adjacent scales on both sides and to the rear, and extends forward on the right side only, narrowing towards the superciliary ridge. This mark appears to be anomalous, for it is absent in all specimens other than the holotype. According to Valdivieso and Tamsitt (1963:31) living animals of this species are bright green.

RANGE. (Text-fig. 1). Records of *Uracentron werneri* are from the upper Río Orinoco valley in Venezuela, and from near the western tributaries of the Orinoco in Colombia.

MATERIAL EXAMINED. *Venezuela* : Amazonas, Alto Orinoco S.M.F. 11203 (holotype). *Colombia* : Metá, near Macarena, Río Guayabero A.M.N.H. 91755 ; Vaupes, Cerro Yapopoda M.C.Z. 67982. Published records from Colombia are Caquetá (Dunn, 1944 : 89), and near the Macarena Mountains, Metá (Valdivieso and Tamsitt, 1963 : 31).

Uracentron flaviceps (Guichenot)

Doryphorus Azureus, variety Duméril, 1851, p. 85.
Doryphorus flaviceps Guichenot, 1855, p. 26 (type locality : Sarayacu, Peru).
Doryphorus castor Cope, 1870, p. 556 (type locality : Pebas, " Ecuador ", now Peru).
Uranocentron flaviceps O'Shaughnessy, 1881, p. 245.
Urocentron flaviceps Boulenger, 1885, p. 183.
Urocentron castor Boulenger, 1885, p. 184.

HOLOTYPE. No. 6682 in the Muséum National d'Histoire Naturelle, Paris. Collectors, Castelnau and DeVille.

CHARACTERISTICS. The supraocular scales are variable ; usually there is an inner row of four or five transversely widened scales, and an outer row of three or four scales that are about half as large as those of the inner row, with a single row of scales between the outer row and the superciliaries.

The dorsal nuchal scales are somewhat conical and keeled, with tiny granules in between. These grade laterally into smaller, but otherwise similar scales on the sides of the neck. The dorsal body scales are larger, imbricate, and distinctly keeled, largest in the sacrolumbar region. The lateral body scales are a little smaller, but otherwise similar to the dorsals. The ventrals are smooth, or faintly keeled, especially in the pectoral region. Scale counts are given in Table I.

The tail is very flat and wide, almost leaf-like, with 30 to 38 whorls of moderately large, spinose scales. A whorl halfway between the vent and the tip of the tail contains 9 to 11 scales. The tail is 0·48 to 0·63 (mean 0·50) times as long as the head and body.

The largest male examined is 128 mm. snout-vent length, the largest female is 87 mm.

Colour in preservative : juveniles and females are a rich, dark brown above, with numerous small, light spots; the spots are light bluish on the head, forelimbs, and anterior part of the body, becoming yellowish on the posterior part of the body, hind limbs, and tail. In juvenile males the light spots tend to be absent from a crescentric band across the nape, leaving a solid, dark band. The throat in females and juvenile males is light bluish with brown spots that may be arranged in irregular, oblique rows ; other ventral surfaces are light grey. In adult males the light bluish spots of the head and neck increase in extent, and join one another until the head and neck have small brown spots on a bluish background. The dark brown nuchal band becomes conspicuous, and is bordered behind by a light, bluish band. On the remainder of the body, limbs, and tail the light spots become obscure or disappear entirely, leaving a uniform dark brown surface. The ventral surfaces become brown as well, except for the chin and throat, and the ventral surface of the tail where some yellow spotting usually remains.

According to my field notes of 7th August, 1961, an adult male of 88 mm. snout-vent length, obtained 39 km. NNE of Oxapampa, Dept. Pasco, Peru (now L.A.C.M. No. 39161) had the following colour in life : dorsum of body, limbs, and tail very dark brown, finely punctate with yellow on limbs and sides of body ; head reddish-brown mottled ; collar a wide, dark brown band bordered behind by a yellow band ; chest and venter of limbs iridescent blue-green ; tail reddish below ; throat dirty yellow. Another male, 114 mm. snout-vent length, from the same locality, had the same pattern, but with colours more intense, and the head was bright reddish. After six years in preservative the reddish and yellow colours have become light bluish-green. Guichenot (1855, pl. 3, fig. 2) gives a coloured illustration of the holotype.

RANGE. (Text-fig. 2). Records of *Uracentron flaviceps* are from the western part of the Amazonian Basin in northwestern Brazil, southeastern Colombia, eastern Ecuador, and eastern Peru. The species occurs together with *U. guentheri* in Peru, and with *U. azureum* in Brazil.

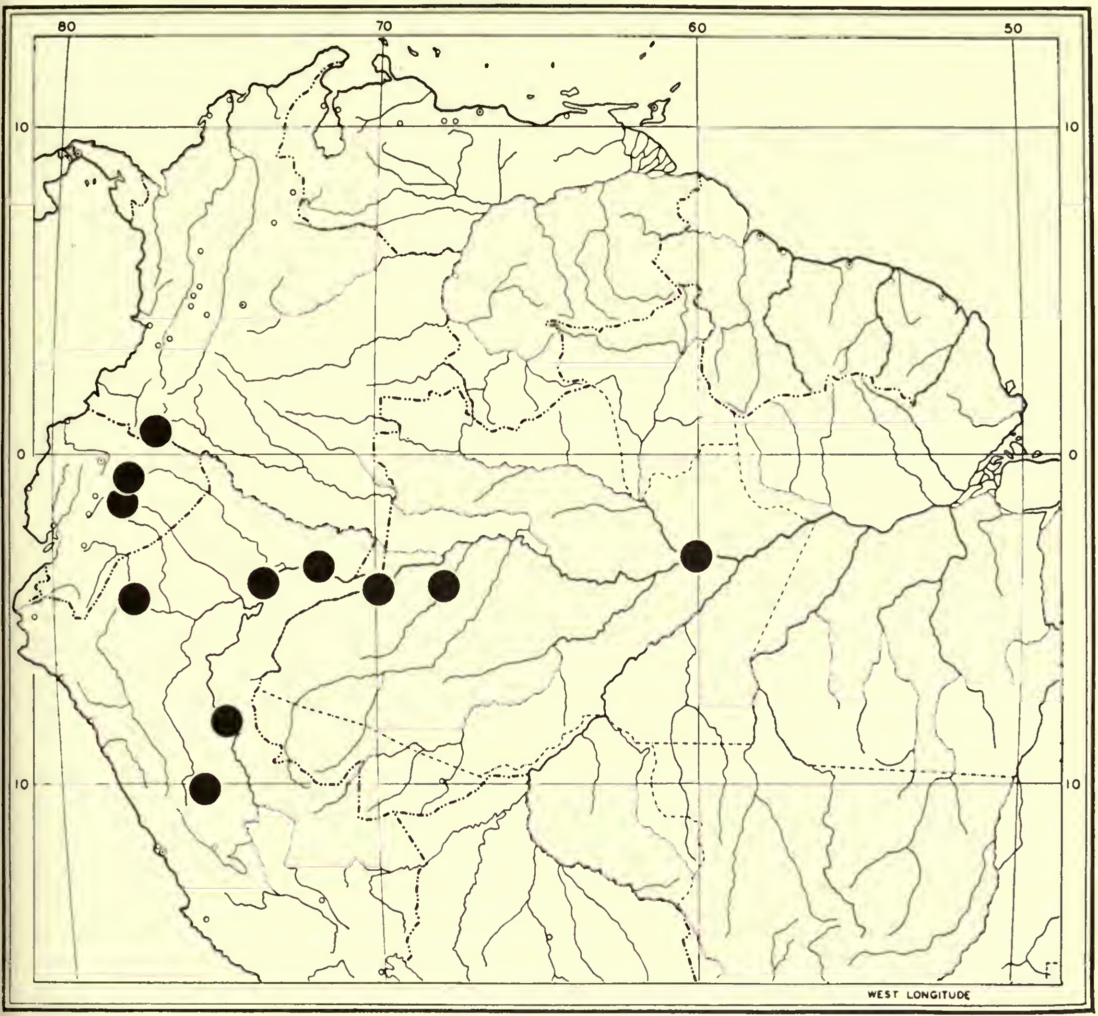

FIG. 2. Map of northern South America showing localities for *Uracentron flaviceps*.

REMARKS. In his description of *Doryphorus castor*, Cope (1870 : 55) used as the principle diagnostic character the presence of the nostril between two scales rather than within a single scale. Boulenger (1885 : 184) recognized *U. castor* as a valid species, but called attention to its close similarity with *U. flaviceps*. Mr. E. V. Malnate has examined the holotype of *U. castor* (A.N.S.P. 11303), and compared it with specimens of *U. flaviceps* from eastern Peru. He has informed me (*in litt.*) that contrary to Cope's description each nasal opening is within a single scale, and in this and in all other details of scalation and colour pattern the specimen is indistinguishable from *U. flaviceps*.

In his list of the type specimens of lizards in the Paris Museum, Guibé (1954 : 42) incorrectly considered *Uracentron flaviceps* to be a synonym of *U. azureum*.

MATERIAL EXAMINED. *Colombia* : Amazonas, Leticia F.M.N.H. 83038, 78384–5 (2 exs) ; Putumayo, Santa Rosa de los Kofanes, upper Río Guamues F.M.N.H. 165828. *Ecuador* : Sarayacu M.H.N.P. 6882 (holotype), B.M.N.H. 80.12.8.56 ; Canelos B.M.N.H. 80.12.8.57–9 ; Pastaza River M.C.Z. 37270 ; Napo, Santa Cecilia M.C.Z. 92519 ; no specific locality Z.M.B. 9988. *Brazil* : Amazonas, Río Madiera A.M.N.H. 57207 ; Amazonas, Manaus N.H.M.P. 92.291 ; Amazonas, Rio Jutaí Z.M.B. 30973 ; Amazonas, Rio Solimoẽs N.R.M.S. 3342 ; Amazonas, Lago Calado S.M.F. 30304/5.1. *Peru* : Loreto, Iquitos A.M.N.H. 56408, N.M.W. 13929 (2 exs), 13930, F.M.N.H. 45487 ; Loreto, Prov. Ucayali, Yarinacocha F.M.N.H. 45484, 56064 ; Loreto, Prov. Ucayali, Pucalpa F.M.N.H. 56061–3 ; Loreto, Prov. Bajo Amazonas, Quidtococha F.M.N.H. 45485–6 ; Loreto, upper Ucayali A.M.N.H. 71101–2 ; Loreto, Pebas A.N.S.P. 11303 (holotype *Doryphorus castor*) ; Pasco, 39 km NNE of Oxapampa L.A.C.M. 39161 ; Loreto, Pongo Manseriche, Marañon valley A.M.N.H. 56409 ; between Apaga and Nieva A.M.N.H. 57206. No specific locality B.M.N.H. 69.5.21.57.

Species Referred Erroneously to ***Uracentron***

Urocentrum meyeri was described by Werner (1900 : 4) from Lima, Peru, and included by Burt & Burt (1933 : 49) in their list of South American lizards. The holotype and only specimen was destroyed in the Dresden Museum (No. 1764) during the last days of World War II. However, the description contains details that are sufficient to identify the specimen as belonging to the genus *Stenocercus* rather than *Uracentron*.

The upper head scales are smooth, the interparietal scale small, and there is a projecting auricular scale. The tail is flattened, but scarcely wider than the sacral region, with spiny scales in rings, and is a little longer than the head and body length : total length 131 mm., tail length 77 mm. These are all characteristics of the spiny-tailed species of *Stenocercus: atrigularis*, *roseiventris*, *marmoratus*, *crassicaudatus*, *carrioni*, and *simonsi*. Additional details in the description, and the type locality indicate that the specimen may have been one of *Stenocercus crassicaudatus*. The sides of the neck have two converging folds, a postympanic and an antihumeral fold, with a horizontal fold between them ; the dorsal scales are small and granular. A median dorsal crest is not mentioned, and presumably was lacking. The ventral scales are said to be similar to the dorsals, but faintly keeled, almost smooth. Only the faintly keeled ventrals are not characteristic of *S. crassicaudatus*. Although there are no records of *S. crassicaudatus* from Lima, the species does occur inland from Lima at higher elevations. The exact identity of Werner's species may never be known, but in any event it is clearly not referrable to *Uracentron*.

Burt & Burt (1933 : 49) also included in their checklist of South American lizards the name *Urocentron palluma*, which they credited to Tschudi (1846 : 35). However, it is clear from Tschudi's own treatment in his *Fauna Peruana* (incorrectly cited by Burt & Burt as 1845), and in an earlier work (Tschudi, 1845 : 157–8) that he is referring to *Phymaturus palluma*, which Tschudi correctly attributes to Molina (1782 : 217). Tschudi listed *Phymaturus* Gravenhorst as a subgenus of *Urocentron*, and gave as its only species in Peru " *U. palluma* Tschudi ". Although he followed the species with his own name, he listed *Lacerta palluma* Molina in its synonomy. Burt & Burt's error is clearly that of accepting Tschudi's placement of *Phymaturus palluma* in the genus *Urocentron*, and, apparently because Tschudi followed the species name with his own, considering Tschudi to be its author. *Phymaturus* is a valid, monotypic genus, containing only the species *palluma*, and quite unrelated to *Uracentron*. It differs from the latter in many ways, including the presence of tricuspid premaxillary teeth, preanal pores in males, a small interparietal scale, and a rather slender, somewhat spiny, autotomic tail.

Relationships Within *Uracentron*

Uracentron flaviceps stands apart from the other three forms of *Uracentron* as the most distinctive species. Compared with the others its tail is much flatter and wider, with smaller, less distinctly spinose scales. Its body scales are larger and consequently fewer in number around the middle of the body, and more distinctly keeled. *U. flaviceps* also attains a greater maximum size.

Uracentron azureum, *U. guentheri*, and *U. werneri* are very similar in the form of their body and tail, and in scalation. *U. guentheri* differs from *azureum* and *werneri* in having greatly expanded, band-like supraoculars, and *U. werneri* differs from *azureum* and *guentheri* in having smooth dorsal scales in the sacrolumbar region. The most obvious differences among the three are their colour patterns : bold black cross-bands usually followed by a bold reticulum in *azureum*, a finer reticulum with narrow cross-bands on the neck in *guentheri*, and solid or faintly spotted in *werneri*. The most extreme example of breaking up of the posterior cross-bands into a reticulum in *azureum* does not approach the pattern of *guentheri*, but transitional stages between the two are not difficult to imagine. The pattern of *werneri* might result from an overall darkening of the pattern of *guentheri*.

The ranges of *U. azureum*, *U. guentheri*, and *U. werneri* are not known to contact one another, or to overlap. With the acquisition of more specimens from intermediate areas it may become possible to determine whether or not any two, or all three of these species intergrade. Until that time the best course would seem to be recognition of three separate species.

1	Tail very strongly depressed. More than 25 whorls of caudal scales from base to tip of tail. Dorsal body scales, including nuchals, distinctly keeled . .	***flaviceps***
–	Tail moderately depressed. Not more than 25 whorls of caudal scales from base to tip of tail. Dorsal scales of neck and anterior part of body smooth . . .	2
2	Four or five band-like supraoculars separated from superciliaries by one row of small scales, or in contact with superciliaries	***guentheri***
–	Supraoculars variable, but those enlarged separated from superciliaries by at least two rows of small scales	3
3	Dorsal body scales in sacrolumbar region obtusely keeled. A bold dorsal pattern of black cross-banks or anterior cross-bands and posterior reticulum . .	***azureum***
–	Dorsal body scales of sacrolumbar region smooth. Dorsum solid gray-brown, or faintly spotted	***werneri***

STROBILURUS Wiegmann, 1834, Herp. Mex., p. 18

Type species *Strobilurus torquatus* Wiegmann.

Diagnosis. *Strobilurus* is a member of the tropidurine group of South American–West Indian iguanid lizards. It was not initially included in that group because I had no data on the structure of the skeleton (Etheridge, 1964 : 629). I have since determined, however, that a large sternal fontanelle is present, and on the basis of this and other osteological and integumentary characteristics, *Strobilurus* is clearly a member of the tropidurine group. Within the tropidurines *Strobilurus* is probably most closely allied to *Uracentron*, *Tropidurus*, *Plica*, and *Platynotus*, all of which have a very large interparietal sacle. The tail of *Strobilurus* is autotomic, about as long as the head and body, and provided with unequal whorls of spinose scales. In *Uracentron* the tail is about half as long as the head and body, and is not autotomic. In the other genera the tail is considerably longer than the head and body, and autotomic. Some species of *Tropidurus* have a moderately spiny tail due to sharp, projecting mucrons, but the spines are not nearly as well developed as they are in *Strobilurus*. Among other South American iguanids some species of *Stenocercus* also possess a tail about equal to the head and body length, and provided with unequal whorls of stout, spinose scales. However, the interparietal scale of *Stenocercus* is very small, or absent entirely.

Characteristics. Upper head scales polygonal, juxtaposed, with a distinctly granular surface. Supraorbital semicircles not well differentiated as such. Three pairs of frontals in contact between the orbits, preceded by two or three larger prefrontals and frontonasals on each side. Two rows of enlarged supraoculars, four or five scales in each row. Those on the inner row a little wider than long and separated from the supraorbital semicircles by two rows of smaller scales ; those on the outer row separated from the superciliaries by two rows anteriorly and one row posteriorly. Interparietal scale very large, about one third as wide as the head, narrowing anteriorly, and as wide as to a little wider than long. A median " eye " present anteriorly in the interparietal scale, and often a median pit followed by a median groove posteriorly. Nasal scale large, dorsolateral in position, with a small, dorsally directed nostril in the posterior part of the scale. Nasal separated from rostral and upper labials by a single row of scales. Two rather small but strongly convex canthals. Canthals followed by five or six elongate, curved superciliaries, each of which overlaps the one behind, these in turn followed by three shorter superciliaries that overlap in the opposite direction. Several polygonal scales in the postnasal-loreal-preocular region. An elongate subocular narrowing anteriorly, with a keel along its upper margin. Loreolabials in a single row below the nasals, two rows below the loreal region, and one row between the subocular and upper labials. Temporals imbricate, obtusely keeled. Tympanum large, about equal to eye opening, with two flat, projecting scales in front. Upper labials more or less rectangular. Lower labials about one and a half times wider than upper labials. No enlarged postmentals. Gulars smooth, imbricate, reduced in size medially and posteriorly.

A row of scales aligned mid-dorsally from occiput to base of tail, its scales slightly larger than, but otherwise similar to adjacent scales, forming a low denticulation in individuals over 100 mm. snout-vent length. Dorsal nuchals rhomboidal, imbricate, sharply keeled, the keels rising to sharp mucrons. Lateral nuchals smaller, spinose along the lateral nuchal folds. Dorsal scales of body rhomboidal, keeled, imbricate, shortly mucronate, the keels forming oblique lines that converge posteriorly toward the dorsal midline. Lateral body scales slightly smaller, but otherwise similar to the dorsals. Ventral scales smooth, imbricate, about one and a half times as large as the dorsals.

Tail about as long as the head and body, and autotomic. Base of tail slightly depressed and a little wider than the sacral region, with eight equal whorls of large, sharply keeled, and strongly spinose scales. Remainder of tail cylindrical and much narrower than the base, with scales of unequal whorls that correspond to the autotomy segments of the vertebral column. Anteriorly each segment with a ventrally incomplete anterior ring of small, smooth scales, and posteriorly an additional ventrally incomplete ring of small scales added to the anterior border of each segment.

Dorsal scales of forelimb rhomboidal, keeled, imbricate, about as large as dorsal body scales. Ventral scales of forelimb smaller, smooth, imbricate. Dorsal scales of hind limb sharply keeled and spinose, similar to but much smaller than spinose scales of tail. Postfemoral scales reduced, keeled, imbricate. Scales of palms and soles sharply keeled and mucronate, some of them tricarinate and tridenticulate. Subdigital lamellae tricarinate and tridenticulate.

A transverse fold extends across the throat just posterior to a line even with the tympani, but scales within fold not differentiated from adjacent gulars. A pair of short, deep, antihumeral folds enclosing very small scales, widely separated ventrally by about 12 anterior pectoral scales. A dorsolateral fold extends posteriorly from upper border of tympanum about halfway back to shoulder ; a ventrolateral fold begins as a pair of converging folds that meet just posterior to tympanum, and extend back to intercept antihumeral fold.

Scales on top and sides of head with numerous scale organs. Dorsal scales of body and limbs with one to three scale organs on the free edge, or none at all. Caudal scales with three to eight scale organs on each side of the keel, along the free edge. No femoral pores or preanal pores.

Strobilurus torquatus Wiegmann

Strobilurus torquatus Wiegmann, 1834, p. 18 (type locality, Brazil).
Steironotus (*Strobilurus*) *torquatus* Fitzinger, 1843, p. 71.
Doryphorus spinosus Guichenot, 1855, p. 27 (type locality, Bahía, Brazil).
Strobilurus torquatus Boulenger, 1885, p. 181.

SYNTYPES. Nos. 672–3 and 9215 in the Zoologisches Museum der Humboldt Universität, Berlin.

CHARACTERISTICS. Since *Strobilurus* is a monotypic genus the characteristics of *torquatus* are the same as those of the genus. The vertebral scales counted from the occiput to a line even with the anterior surface of the thighs when the limbs are extended at right angles to the body number 39 to 57 (mean, 55·6); the paravertebral scales counted in the same way are 49–72 (mean, 67·6). There are 19 to 29 (mean, 24·1) lamellae under the fourth finger, and 23 to 34 (mean 28·3) under the fourth toe. The tail is 0·93 to 0·95 (mean, 0·94) times as long as the snout-vent length. The largest male examined is 97 mm. snout-vent length, the largest female is 106 mm.

Colour in preservative : the head and neck above are bluish-grey, with bold, black markings. There is a narrow, black crescent on each side where the supraoculars contact the frontals and frontoparietals. A wide crescent extends across the anterior part of the neck from ear to ear, and from this crescent there extends anteriorly a medial bar. On each side a black crescent extends from the interparietal scale down to the angle of the mouth. A wide, black, crescentric collar about six or seven scales wide middorsally, extends down on each side into the antihumeral fold. Behind the black collar the dorsal surface of the body, limbs, and tail is somewhat darker greyish-green, with obscure lighter cross-bands. The chin and throat are marbled light and dark grey, and the belly is light grey. A coloured illustration may be found in Guichenot (1855, pl. 7, fig. 1a), labelled *Doryphorus spinosus*.

RANGE. *Strobilurus torquatus* is known from the states of Pernambuco, Alagoas, and Bahía, Brazil.

REMARKS. Wiegmann described *Strobilurus torquatus* in a footnote (1834 : 18) and the subsequent taxonomic history of the genus and species has been relatively uncomplicated. The species has remained rare in collections.

MATERIAL EXAMINED. *Brazil* : Alagoas, São Miguel M.C.Z. 59275; Bahía, no specific locality Z.M.B. 9215, 672–3 (syntypes), 8272, M.H.N.P. 5085 (2 exs, syntypes of *Doryphorus spinosus*), N.M.W. 13908 (2 exs), B.M.N.H. 62.11.23.50, 1903.10.16.23; Pernambuco, no specific locality B.M.N.H. 88.4.18.6. *South America* : no specific locality M.H.N.P. 6880, N.M.W. 13909 (2 exs), B.M.N.H. xxiii.104a.

TABLE I

	azureum N = 58	*guentheri* N = 6	*werneri* N = 3	*flaviceps* N = 29
Scales along middle of black	105–(118·1)–139	124–(130·8)–139	127–(123·3)–141	74–(80·0)–88
Scales around middle of body	92–(107·0)–120	98–(110·4)–128	98–(105·3)–110	66–(78·2)–88
Subdigital lamellae of fourth finger	25–(28·0)–32	24–(27·4)–30	31–(31·3)–32	25–(29·7)–33
Subdigital lamellae of fourth toe	27–(30·5)–36	27–(29·0)–36	31–(31·6)–34	26–(30·3)–34

TABLE 1. Some scale counts of *Uracentron*. Scales along middle of back counted from occiput to line even with anterior margin of hind limb at right angles to body ; scales around middle of body counted halfway between limb insertions. Mean figures in parentheses. N = number of specimens examined.

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British Museum (Natural History)

Pp. 65–90 ; 6 *Plates* : 2 *Text-figures*

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NIGERIAN LIZARDS OF THE GENUS *AGAMA* (SAURIA : AGAMIDAE)

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SYNOPSIS

The external morphology, distribution and systematics of the species of *Agama* occurring in Nigeria are reviewed. The number and position of the dermal sense organs on the trunk scales are used to help clarify the status and relationships of the five species recognized. *Agama agama benueensis* Monard is shown to be a complex comprising two distinct species, one of which is described as new, the other sympatric with but unrelated to *Agama agama* (Linnaeus). *Agama boensis* Monard is not a valid form; the types are a mixed series of *Agama sankaranica* Chabanaud and *Agama weidholzi* Wettstein.

INTRODUCTION

Until a few years ago it was believed that only three species of *Agama* occurred in Nigeria: the ubiquitous *Agama agama* (Linnaeus) and the two smaller and less common species *A. sankaranica* Chabanaud and *A. gracilimembris* Chabanaud. But in 1963 Dr. Hilary Fry of the Ahmadu Bello University, Zaria drew my attention to the existence of a form which he described as being of similar adult size to *Agama agama* and as occurring on the smaller inselbergs in the Zaria region of northern Nigeria. The adult male was said to be distinguished by four indigo or black, clearly defined blotches on the throat. It was immediately recognized from an examination of an adult male which Fry submitted that this *Agama* was not conspecific with any of the three known species. With the co-operation of members of the staff of his department intensive efforts were made to obtain further examples as well as ecological data. The material resulting from these field studies contained more adult male " blue throats " but not adult females belonging to the same form, instead examples of *Agama sankaranica*, which in the field had been confused with the apparently undescribed form, and gravid females of yet another apparently undescribed agama. The absence in collections of females and immature individuals of this " blue throat " continued until the following year when a Danish zoologist, Dr. Arne Schiøtz, who was working in the British Museum recognized the male blue-throated agama as being similar to ones he had collected in the Western Region. His large series, obtained on inselbergs near Idanre and Igbetti, included both sexes and juveniles and were in the collections of the Zoologiske Museum Copenhagen. A detailed study there of his material enabled me to appreciate the difficulty that other collectors had encountered in the field in distinguishing the females and immature individuals from the superficially similar *A. sankaranica* and to elucidate the intraspecific variation of all the Nigerian forms of *Agama*. The study was extended by referring to type and other material in several institutions and to the British Museum's collections including those acquired during the 1962 Northern Nigeria expedition. Finally the specimens on which Monard based the name *Agama agama benueensis* were borrowed.

The identity and relationships of Monard's *Agama agama benueensis* had not been questioned until Wermuth (1967) in a footnote pointed out that *benueensis* is probably no more than a local variety of *Agama agama agama* differing from it only in minute details of toe length and pattern. The original description of *benueensis*, extremely brief and inadequate, turned out to be based on a mixed series, some of the individuals being conspecific with the Nigerian " blue-throated " form, while others, strikingly different in their pattern and in the position of the nostril and with a lower average midbody count are closely related to *Agama agama* and apparently conspecific with a Nigerian population. The name *benueensis* is here applied to the " blue-throat " form and a lectotype is designated. The information now available on the ecology, morphology, distribution and variation of *Agama agama*, *A. benueensis*, *A. sankaranica* and *A. gracilimembris* is given and a new species is described.

Descriptions are based on the observed variation in the examined material.

Throughout this paper the following abbreviations are used to refer to specimens or collections.

B.M.	British Museum (Natural History)
M.H.N.C.F.	Muséum d'Histoire Naturelle, La Chaux de Fonds
M.N.H.N.	Muséum National d'Histoire Naturelle, Paris
Z.M.C.	Universitets Zoologiske Museum Copenhagen

METHODS AND TERMINOLOGY

The characters used in this study are defined as follows:

Body scales. The shape, size and direction of imbrication of the trunk and flank scales, the extent of the keel relative to the axial length of each scale, from its anterior border to its apex.

Microscopic structure of body scales. The number and position of the " hair-bearing " scale organs on the scales of the mid trunk region were studied by removing a series from the vertebral to the mid ventral row and mounting them according to the method described by Underwood (1957).

Midbody scale count. The number of longitudinal scale rows around the middle of the trunk.

Vertebral count. The number of transverse scale rows along the vertebral line from forelimbs (on a level with the axillae) to hind limbs (groin).

Direction of imbrication of temporal and supratemporal scales. Direction of overlap of the scales in these regions, the regions being defined as: temporal, the area between the anterior rim of the ear and the postocular scales, overlying the temporal fossa and the squamosal and the posterior half of the jugal bones; supratemporals, the scales overlying the supratemporal arcade and the postorbital bone.

Body length. The distance from the tip of the snout to the anterior margin of the vent, measured with dial calipers.

Head length. The distance measured with dial calipers from the tip of the snout to the angle of the lower jaw at the posterior extremity of the articular.

Upper labials. The number of scales bordering the upper lip, counted from the scale adjacent to the rostral to the corner of the mouth.

Lower labials. The number of scales bordering the lower lip, counted from the scale adjacent to the mental to the corner of the mouth.

Lamellae under fourth toe. The number of transversely enlarged scales under the fourth toe from the base of the claw to the junction of the fourth toe with the third toe.

Relative lengths of the toes. Comparisons of the first and fifth and of the third and fourth are expressed as the number of lamellae contained in the difference in lengths when the toes are laid flat and parallel to each other.

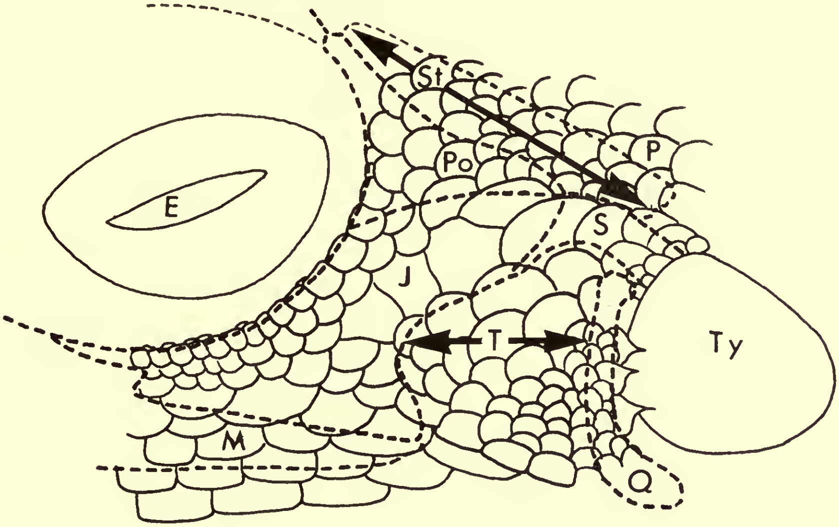

FIG. 1. Supratemporal and temporal areas of *Agama*; underlying bones indicated by broken lines.

E—Eye
J—Jugal
M—Maxilla
P—Parietal
Po—Postorbital bone
Q—Quadrate
S—Squamosal
St—Supratemporal arcade
T—Temporal fossa
Ty—Tympanum

DERMAL SENSE ORGANS

Cohn (1914) was the first person to report on the occurrence of dermal sense organs in *Agama* and he described in detail their histology as well as their external appearance and distribution on various parts of the body. His study was restricted to *Agama colonorum* (= *A. agama*). Subsequently Schmidt (1920) and Preiss (1922) examined the scale organs of other species and genera of lizard, Schmidt extending his studies on reptile receptors to the Gekkonidae, Iguanidae and Agamidae but limiting his investigation of *Agama* to an Asian species *A. sanguinolenta*, which however exhibited several differences from *A. agama*, as described by Cohn, in the number and position of the organs on each trunk scale. It was not until 1937 and 1941 when Scortecci made an extensive survey of the lenticular and " hair-bearing " sense organs in the Agamidae that the density of these receptors and their positions on each scale were shown to have some value as a species character. (The agamid material which

Scortecci used belonged to nineteen genera and eighteen species, his nine species of *Agama* all being African forms but none occurring in West Africa.) But despite the breakthrough afforded by Scortecci's meticulous comparative studies the potential of the receptor character for helping to distinguish agamid species was passed by, yet Underwood (1957) in surveying the scale organs in pygopod lizards had stressed that they would repay further study and Wayne King (1962) had effectively demonstrated their usefulness in sorting out the taxonomy of Caribbean sphaerodactyl geckos. The only attention recently given to these scale organs is by Miller and Kasahara (1967) who have studied their innervation and who remark on the tactile function of the " hair-bearing " receptor.

In species whose mode of life is known correlations might be established between habits and the frequency with which the " hair " bearing organs occur, their position on the scales, their distribution on the body surface and the extent to which the " bristles " project beyond the edge of the scale. An investigation along these lines seems merited but unfortunately through lack of adequate field observations this could not be carried out on West African species of *Agama*.

It has been found in the present study that the species number and the position of the " hair-bearing " organs on the trunk scale do not vary ontogeneticaly, nor sexually, but that there is some individual variation which is discussed under the species. Nor does this character vary geographically, at least not in four of the Nigerian species where material from throughout their known ranges has been examined. Whether there is geographic variation in *Agama agama* receptors has still to be established but none is evident in the Nigerian specimens.

Another apparently reliable taxonomic character not previously employed in keying out agamas is introduced into this study, namely the direction of imbrication of the temporal and supratemporal scales. These two characters, receptors and direction of imbrication, both of which are probably related to the animal's ecology, seem to have greater significance in classification than some of the characters so rigidly adhered to in the past in keys and descriptions of species of agama; certainly the results of studying them in the Nigerian species are encouraging and an extension of study to other groups of agamid lizards may help elucidate the status and relationships of the many forms that have been described.

Agama agama (Linnaeus)

(Map, Pl. 1, figs. c, d; Pls. 4, 5)

Lacerta agama Linnaeus, 1758 : 207.

MATERIAL EXAMINED. NIGERIA, *Sokoto Prov.*, 1 mile north of Kware, 15 miles north of Sokoto B.M. 1962.1609; *Katsina Prov.*, Rimi village, 13 miles South-east of Katsina B.M. 1962.1608; *Kano Prov.*, Birnin Kudu B.M. 1962.1610; *Bornu Prov.*, Maiduguri B.M. 1962.1611, Galtimare village, South of Maiduguri B.M. 1962.1612; *Zaria Prov.*, Kawo, 4 miles north of Kaduna B.M. 1962.1596–98, Kujama, 25 miles South-east of Kaduna B.M. 1962.1599–1603, Zonkwa B.M. 1962.1604 and 1606, Birnin Gwarri B.M. 1967.2207, Galma Fadama B.M. 1967.2208, Old City Zaria

B.M. 1967.2209–2211, River Amethyst, Kaduna Road, Zaria B.M. 1967.2212; *Plateau Prov.*, Jos B.M. 1962.1613–54, 10 miles south of Jos on Miango Road B.M. 1962.1593–95, Shendam B.M. 1962.1574–92; *Oyo Prov.*, Igbetti Z.M.C. R36561, 36567, 36569, 36573, 36565, 36644, 36655, 36745, 36286–9; *Ondo Prov.*, Idanre Z.M.C. R36577–8, 36584, 36586.

DESCRIPTION. Body subcylindrical, little depressed above, between 3·3 and 3·8 times the head length. The body of adult males rather triangular in section, the apex mid dorsal. Nostril on a line connecting the canthal supraciliaries with the rostral/first labial suture, that is on the canthal ridge; situated in the posterior half or third of a strongly swollen, pear-shaped nasal shield and directed upwards, or upwards and outwards. A keel usually present between the nostril and the anterior edge of the nasal. On its posterior margin the nasal forms a suture, generally a broad suture, with the first canthal supraciliary. The supraorbital scales and the scales overlying the frontal and anterior portion of the parietal quite smooth, the other scales on the head keeled, particularly so in juvenile specimens. The direction of imbrication of the scales overlying the supratemporal vacuity is forwards but the direction of the scales covering the postorbital bone alters to downwards and slightly backwards. The scales overlying the temporal fossa, imbricate in the reverse direction and between the two areas and along an oblique line, which marks the position of the squamosal and the posterior limb of the jugal, is a single row of quite strongly keeled juxtaposed scales (Pl. I, fig. c and Text-fig 1). Occipital enlarged, of variable size, its greatest width generally half to three quarters the diameter of the tympanum. Seven to twelve upper labials; a similar number of lower labials. A long, low nuchal crest of approximately fourteen scales but no dorsal crest. A poorly developed caudal crest present in adult males. The shape of the ear roughly a right-angled triangle, the tympanic membrane rather superficial. No conspicuous fringe of long, pointed scales along the anterior border of the tympanum but a few erect scales which in juveniles may be only slightly raised. A row of erect or somewhat spinous scales from the commissure of the lips to immediately behind and below the tympanum where it joins with one or two (in adults invariably two) *round* groups of spinose scales on the swollen area at the angle of the jaws. At the upper posterior corner of the tympanum a less elevated and more elongated group of erect scales is present. Midway between a point half way along the nuchal crest and the lower posterior corner of the tympanum lies a small oval group of spinose scales; in front of and also behind this group a very small group of erect scales usually insignificant but if prominent the longest scales less than half the width of the tympanum. All these groups of erect scales are considerably more pronounced and the scales longer and more spinous in adult specimens, particularly in adult males, and in the juveniles the groups may be quite inconspicuous. A strong gular fold present in both sexes.

Body scales homogeneous, those in the mid dorsal area flattened dorsoventrally, their distal margins rounded, often only feebly keeled and with short mucrones. Scales on the flanks more rhomboidal, particularly in adult males, the keels more pronounced and terminating in upward turning short mucrones; distal margins somewhat denticulate. Scales on either side of the nuchal crest small, barely mucronate, approximately equal in size to those between the neck pit and ear.

The sense organs of each trunk scale are situated at the distal margin or just below the dorsodistal edge of the scale. They are not confined to the area around the base of the mucrone but may extend along the entire distal aspect of the scale. No scale organ on a trunk scale has more nor less than one " bristle ". The number of receptors per scale varies from one to eight and while there is a tendency for the number to increase on the flanks and then diminish towards the venter no definite correlation could be established between the number of organs per scale and the longitudinal scale row although the body scale rows bearing the highest density are invariably between rows ten and sixteen. It is in this region of the trunk that the scales often have a rhomboidal shape with a somewhat denticulated distal margin and each organ is usually situated in an identation. Harris' (1963) statement that sense organs are absent from the ventral body scales is incorrect. Each ventral scale has one but no more than one " hair-bearing " sensory organ at the apex. The smoother scales of the middorsum generally have one to four sensory organs per scale.

Cohn (1914) found only three organs on each of the scales of the back and describes the central one as placed somewhat to one side of the projecting tip of the keel. He reports a similar number of receptors on flank scales and says that the scales on the vertebral line may lack one or both lateral organs. He gives no indication of the origin of his material which he identifies as *Agama colonorum*, and there seems to be a strong possibility that a misidentification accounts for the much lower density of trunk scale organs in his specimens.

Midbody scale counts of sixty-four Nigerian examples 59–77, the mean for thirty-five females being 68·2 and for thirty males 66·2; vertebral count 38–55. Mature males with eight to twelve, usually ten preanal pores. Eighteen lamellae under the fourth toe. First toe shorter than the fifth by two to seven (usually three to six) lamellae. Third toe shorter than fourth toe by one to two lamellae, very exceptionally subequal. Tail approximately twice the body length, depressed at the base and particularly so in adult males, its scales strongly keeled and mucronate and arranged in whorls.

INTRASPECIFIC VARIATION. Loveridge (1936) in discussing intraspecific variation in *Agama agama* remarked on the extraordinary wide range of midbody count, 60–80, quoted by Boulenger (1885). Presumably Boulenger's counts were based solely on the material that was available in the British Museum at that time, namely twenty-one West African examples many of which bore no more precise locality than " West Africa ", and eight Angola and South West Africa examples, in other words a small sample from only a very limited portion of the range of the species. In the 1936 publication Loveridge demonstrated without regard to any sex difference a gradual reduction in the same count from east to west (Uganda to Senegal) and in the belief that populations occurring west of Ghana have a considerably lower average count he suggested recognizing these individuals as belonging to a distinct race, *savatieri* Rochebrune. The recognition of a western race based solely on this character was ill conceived and hasty, particularly in view of Loveridge having at his disposal only one individual from Ghana and none from the 1,000 mile stretch between Ghana and the Cameroun. In 1956 Grandison in reporting on over one hundred *Agama agama* obtained in West Africa west of Ghana remarked on a southwest to northwest reduction from 68 to 60 in their average midbody count (range of the entire series 56–76). She assigned the individuals to *A. agama savatieri*, having overlooked the statement in Loveridge's later paper (1941) that Hallowell's name *africana* has priority over *savatieri*.

Daniel's (1961) counts (M 61·6 ♂ : 65·1 ♀) on twenty adult Liberian individuals which he identified as *A. agama africana* agree favourably with those given by Loveridge (1936, 1941) for Liberian material but suggest that Loveridge's samples in which the average number of scales round the body was sixty-two probably consisted mainly of males.

The range of variation in midbody count in the sixty-five Nigerian examples studied here runs almost the whole gamut of the variation said to occur in *africana* but the average number of scales in males and females are intermediate between those quoted by Loveridge for Cameroun and Uganda individuals of the nominate form and those given by Loveridge, Daniel and Grandison for examples identified as *africana* and obtained west of Ghana. The Nigerian, Ghanaian and eighteen of the Senegal counts shown in the map are for adult specimens in the British Museum collection.

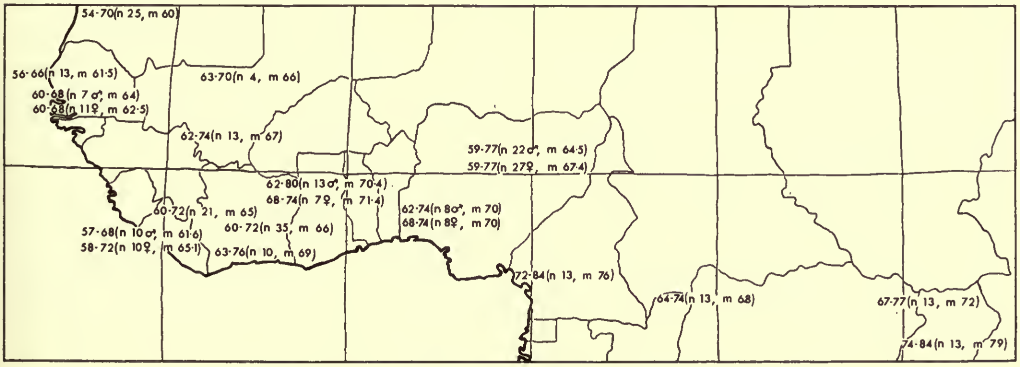

FIG. 2 Geographic varation in midbody count in *Agama agama*.

Thys van den Audenaerde (1963) in his study of Congolese species of *Agama* examined large samples of *A. agama* from the Congo and compared his findings with those of other authors for specimens from all regions in the range of the species. His thorough review of the pertinent literature available on *Agama agama* emphasizes the clinal sequence in midbody count from east to west although his argument is to some extent weakened by blind acceptance of identifications by others, to unequal sampling and to his not distinguishing between the counts for males and for females. He includes in his range of variation in *A. agama* a specimen from the Bauchi Plateau with ninety-two midbody scales that Grandison (1956) identified as *A. sankaranica*. While the individual is not available for re-examination it seems more than likely that it was incorrectly identified and is actually an example of *A. benueensis*, a species closely related to *sankaranica* and in its juvenile livery resembling *sankaranica* but with a considerably higher midbody count. An Aïr specimen with a low count of 58 was also mentioned by Grandison (1956) but excluded from the table of means; it too was probably incorrectly identified and may be an example of the large scaled species *Agama boueti* Chabanaud. This species was described from Gao on the Niger. Examination of type material shows that its trunk receptors are similar in number and position to those of *A. bibronii* Duméril of North West Africa and are quite unlike any other West African form.

Thys van den Audenaerde maintains that development of the keel and mucrone is correlated with body count, the lower the count the stronger the keeling, but I can establish no such link in the Nigerian material where variation in this character seems to be related to the proximity of sloughing. He further comments on the geographical variation that occurs in *A. agama* colouration, in particular of the head, throat and tail, which is perhaps correlated with the clinal gradient in scaling and he draws attention to Angolan intermediates between the nominate race and the Angolan race *mucosoensis*. A similar cline in the development of the nuchal crest which both Stejneger (1893) and Thys van den Audenaerde (1963) have suggested exists, has not yet been effectively demonstrated. Much more quantitative data on large samples from throughout the range of the species would have to be compared, sex with sex, if a true picture is to emerge. Meanwhile the only East African figures available are those of Stejneger based on only six Kenya examples, and of Barbour and Loveridge (1928) for eighteen adult Usambara specimens and in neither case is the sex or the proportion of the sexes stated. Since in Nigeria at least, there is a sex difference in the length and height of the crest, the spines being fewer and shorter in the females, the East African figures are not necessarily comparable with those for twenty adult male Nigerian individuals (13–17 : M 14·9).

Thus the abundance of races of *A. agama* that have been described reflects not the occurrence of legitimate geographically localized subdivisions but accidents of sampling or more likely the work of splitters. There would appear to be no evidence of geographic isolates but only of marked individual variation *within* a population and Thys van den Audenaerde's conclusion that *Agama agama* is a large polymorphic species rather than a polytypic species would seem to be the logical one.

COLOUR. Immature individuals and adult females are similar in colouration. In their reproductive colour phase the head is a medium brown or brown with green tinges, the back fawn or brown with darker brown marks of variable shape and position but often in the form of rather indistinct diamond-shaped outlines along the vertebral region. The upper part of the head, the temporal region and the neck have pale green spots and short longitudinal stripes of the same colour. The undersurfaces are a grey-white. Mature males that are dominant over territories are characterized in their reproductive colour phase by an orange head and neck, indigo blue body and by a median orange segment on a black-tipped tail. Other colour phases occur and these as well as the reproductive colour phase are admirably and fully described by Harris (1964).

ECOLOGY. In Nigeria wherever the savanna and forest have been disturbed by human agency, bridges built, houses and shacks erected, trees felled, rubbish dumped, *Agama agama* seems to have established territories. It is very much a commensal of man and is common around native houses, farm buildings, litter, wood piles and along paths. The species is also common in the boulder strewn country flanking the road from Jos to Miango. Schiøtz (personal communication) says that its habitat preferences do not include flat uniform savanna, nor large rocks, nor dense forest but as soon as such areas acquire human habitations or are in other ways disturbed by man *Agama agama* takes up residence. While this is largely true, the rocky mass of Kujama Hill south of Kaduna supports a number of *Agama agama* yet on the bare rock surfaces of the vast gneiss domes 1,000–3,000 ft. high at Igbetti and Idanre *Agama agama* is absent, its place being taken by *Agama benueensis*.

RANGE. Senegal to Ethiopia, southwards to Tanzania and Angola.

Agama paragama sp. n.

(Pl. 1, figs. a, b; Pls. 4, 5)

Agama agama benueensis Monard 1951 : 131 (part).

MATERIAL EXAMINED. HOLOTYPE: NIGERIA, *Zaria Prov.*, ½ mile Southwest of Ahmadu Bello University, Zaria City, collected by C. H. Fry from Parkia tree on 17.ii.1964, B.M. 1967.2215 ♀.

PARATYPES: NIGERIA, *Zaria Prov.*, same locality as holotype B.M. 1967.2216, Mile 7, Zaria Road B.M. 1967.2214, Mile 5, Zaria Road B.M. 1967.2213, Ahmadu Bello University campus B.M. 1967.2217, no information, probably in vicinity of Zaria City B.M. 1967.2218, Birnin Gwarri, 62 miles Southwest of Funtua B.M. 1968.497, Zaria City B.M. 1968.482–483, Veterinary Unit, Zonkwa B.M. 1962.1605, B.M. 1962.1607; *Bornu Prov.*, Potiskum B.M. 1968.498, Yo B.M. 1968.496; *Plateau Prov.*, Naraguta, Jos B.M. 1968.484–485. CAMEROUN, Bangouvé M.H.N.C.F. 1162, Rei Bouba M.H.N.C.F. 1432, 1440, 1459, Mayo Sala M.H.N.C.F. 1374, Ngaouyanga M.H.N.C.F. 965 (six of the paralectotypes of *Agama agama benueensis*.)

These individuals differ from *A. agama* not only in body size, proportions, greater spinosity and in lower average midbody and vertebral counts but in an absence of sexual dimorphism in size. They resemble *A. agama* in the position of the nostril being on the canthal ridge and in having multiple sense organs on the distal edges of the scales of the flanks and the two forms are undoubtedly closely related but being sympatric in Nigeria specific status is given to *paragama*.

Relatively few examples of *paragama* have been collected and the form is so far known only from northern Cameroun and from the Northern Region of Nigeria, although one specimen obtained by C. H. Fry in a crevice 10 ft. up a Terminalia tree in the Botanical Gardens, University College, Ibadan was thought by him to belong to this form; the specimen has not been seen by me. Although situated in the high forest belt Ibadan has many clearings that have the character of cultivated savanna woodland and support typical savanna species. Schiøtz (1963) describes the vegetation of the University College campus as " dry forest and culture savanna ". It is possible that where suitable habitats are available this species, like *Agama benueensis*, penetrates the Western Region's forest belt.

Description of Holotype. Body subcylindrical, depressed above, 3·6 times the head length. Nostril on the canthal ridge, situated in the posterior half of a swollen, pear-shaped nasal shield and directed laterosuperiorly. Nasal keeled from its anterior tip to the upper rim of the nostril, forming a suture on its posterior margin with the first canthal supraciliary. The supraorbital scales and the scales overlying the frontal and the anterior portion of the parietal quite smooth, remaining head scales keeled. The direction of imbrication of the supratemporal scales is forwards and slightly upwards; anteroventrally the scales overlying the postorbital bone face downwards and backwards. The scales immediately in front of the ear, that is those overlying the temporal fossa, imbricate in the reverse direction to those covering the lower postorbital and between the two areas and along an oblique line marking the position of the squamosal and posterior limb of the jugal is a single row of large, keeled, juxtaposed scales. Occipital enlarged, its greatest width equal to three-quarters the horizontal diameter of the tympanum. Upper labials 8 : 9 (one divided); lower labials 9 : 10. A short but conspicuous nuchal crest formed from nine, long, conical scales, the longest equal to three-quarters the width of the tympanum; no dorsal nor caudal crest. Ear triangular. On anterior margin of ear a fringe of two to three long, pointed scales, on upper posterior border one long, pointed scale surrounded by several erect scales (this group barely developed on left side of head). At the posterior extremity of the lower jaw, that is behind and below the ear, a small, round group of spinose scales of which one scale is three to four times longer than the others. A similar group immediately above. Between a point midway along the nuchal crest and the lower, posterior corner of the tympanum lies a prominent round tuft of long spinose scales the longest scale three-quarters the tympanic diameter; in front (right side only), and also behind, a small, round but insignificant group of erect scales. (The lengths of the scales comprising the nuchal crest and the groups of spinose neck and ear scales are considerably longer and more pronounced in male specimens: see note on variation.) A well developed gular fold.

Body scales homogeneous, the longitudinal rows converging towards the midline, scales on the dorsum and flanks equally strongly keeled and mucronate; the mucrones of the flank scales rather broad at their base, tapering rapidly and rising at an angle to the scale. Distal margins of the body scales rounded on each side of the mucrones. Ventral scales smooth. Scales on either side of the nuchal crest with strong, compressed keels and long, almost erect, mucrones, the scales at least twice the size of those between the neck pit and ear.

The maximum number of sense organs on the middorsal and flank scales is nine, the minimum three. They are situated just under the dorsodistal margin and may extend as far as the " shoulders " of the scale. No scale organ on a trunk scale has more nor less than one " bristle ". The highest density of receptors on midtrunk scales occurs on longitudinal rows 3–5. Each ventral scale bears a receptor at its apex.

Midbody scale count 60, vertebral count 30, eighteen lamellae under the fourth toe. First toe four or five lamellae shorter than the fifth toe, third toe half to one lamella shorter than the fourth.

Tail one and a quarter times body length (tip of tail missing), depressed at base, only very slightly compressed distally, its scales keeled and strongly mucronate and arranged in whorls.

Length of body 94·0 mm.

VARIATION. The following variation in meristic characters in the paratype series was noted. Nigerian individuals: midbody scale count 50–66 (M 58·5), vertebral count 26–34 (M 30·1), number of lamellae under the fourth toe seventeen to twenty-one, first toe shorter than fifth toe by between three and five lamellae, third toe half to two, usually one to two lamellae shorter than fourth toe. Differences in the development of the rosettes of neck and ear spines and in the lengths of the scales forming the nuchal crest are attributable to sex and maturity, in adult males the longest of the pointed nuchal crest scales being as much as equal to the width of the tympanum, likewise the most prominent scales in the neck tufts, whereas in females they are less than three-quarters the diameter of the tympanum. The number of scales forming the nuchal crest varies from eight to ten, the usual number being eight. The density and distribution of " hair-bearing " receptors on the midbody scales of the paratypes is similar to the holotype. Sex dichromatism is discussed below. The tail of the adult male is considerably more compressed than that of the female and has a slight crest; the base of the tail is depressed but not to the same extent as in *Agama agama*.

Juvenile *A. paragama* in which the neck and ear rosettes and nuchal crest are insignificant can be readily distinguished from young individuals of *A. agama* by the relative size of the scales above and below the central neck rosette and by the roundness of the rosette. Further distinguishing features are the pattern, lower vertebral count, gradual tapering of the tail and less depressed base to the tail.

All the Cameroun examples, except an adult male (Mayo Sala M.N.H.C.F. 1374), fall within the range of variation in midbody count of the Nigerian individuals but they have a slightly higher number of transverse rows on the trunk, their vertebral count being 36–38. The Mayo Sala example with seventy-two midbody scale rows is well outside the normal range of variation in the species yet in its other morphological characters it agrees with *paragama*.

COLOUR. Male. In life the upper surfaces of the body and limbs of the adult ♂ are a metallic blue with white flecks. On the back the flecks tend to be arranged in narrow transverse lines, no more than one scale in width, with approximately eight lines between fore and hind limbs. The vertebral zone is whitish, the head chalk white, the proximal two-thirds of the tail whitish, the tail tip black. Except for the whitish areas the general appearance of the ♂ is rather similar to the reproductive colour phase of a male *Agama agama*. Harris (1964) describes in detail the various colour phases of both ♂ and ♀ *Agama agama* and while he refers to a geographical variation in the colour of the head of adult males, northern individuals (Kano) having a deep yellow while more southern populations have either orange or vermilion, he makes no mention of any adult male *agama* in which the orange or yellow tones are replaced by white.

FEMALE. None of the colour phases described by Harris for female *A. agama* occurring in Nigeria corresponds to, or in any way approaches the colour pattern of female *A. paragama* which is characterized by four or five pairs of more or less clearly defined, large, round, brown spots on a lighter brown (orange in life) background on the dorsum between fore and hind limbs. In those specimens in which the spots are ill-defined the lateral halves of the spots are indicated by narrow, dark brown outlines. The flanks and the upper surfaces of the limbs and tail are of a similar shade of brown to the spots; the head is mottled brown. In both sexes the throat, and in some specimens also the sides of the neck and chest, has a dark network on a cream ground which takes the form of isolated, round, cream spots and is dissimilar to the gular pattern of *A. agama* which tends rather to consist of a longitudinal arrangement of dark lines or blotches (Harris, 1964). The distinctness of the gular spotting does not appear to bear any relation to the maturity or sex of the individual, for example one gravid female has a pronounced pattern while in another a pattern is barely discernible. No pattern whatsoever is present on the throat of one adult male but a distinct network is present in another mature male

Adult female *paragama* are larger and considerably more robust than female *agama*. Three gravid female *paragama* vary in body size from 96–107 mm. while the gravid female *agama* examined in this study vary from 86–91 mm. Harris (1964) records 97 mm. as the average body length of sixty-eight Nigerian adult female *agama* and Chapman & Chapman (1964) regard all Ghanaian female *A. agama* of about 90 mm. as mature. Adult male *paragama* are considerably smaller (99–108 mm.) than mature male *agama* obtained in the same general area (107–137 mm.).

ECOLOGY. Little information on the ecology of *paragama* is available. Fry (in litt.) states that the species is to be found on the trunks and lower limbs of shade trees and collectors have suggested that it occupies a different ecological niche from *A. agama* but only the specimens collected at Mile 7 Zaria, Potiskum and Birnin Gwarri bear information that suggest an arboreal existence (Mango and Parkia trees); the Yo specimen, a juvenile, was taken on the walls of a house and the rest of the examined material have no biotope data.

RANGE. West Africa: Northern Region of Nigeria to northern Cameroun.

Agama benueensis Monard

(Pl. 2, figs. a–d; Pls. 4, 5)

Agama agama benueensis Monard, 1951 : 131 (part).
Agama agama boensis Monard, 1951 : 130 (part: males).
?*Agama sankaranica*: Grandison, 1956 : 231 (part: Bauchi specimen).

MATERIAL EXAMINED. CAMEROUN, Upper Benue, Ngaouyanga M.H.N.C.F. 956–7, Sakdjé M.H.N.C.F. 1269, Mayo Sala M.H.N.C.F. 1373, Rei Bouba M.H.N.C.F. 1442, 1460, 1517 (seven of the paralectotypes of *A. a. benueensis*), Ngaouyanga M.H.N.C.F. 961 (designated lectotype of *A. a. benueensis*). NIGERIA, *Oyo Prov.*, Igbetti Z.M.C. R 36342, 36345, 36347–51, 36353, 36389, 36392, 36394, 36397, 36399, 36401, 36599, 36601–12, 36614–20, 36661–2, 36702–3; *Ondo Prov.*, Orosuta, Idanre Z.M.C. no number, Idanre Z.M.C. R 36576, 36579, 36580–2, 36585, 36588–9; *Zaria*

Prov., R. Amethyst, Kaduna Road B.M. 1967.2234–8, B.M. 1967.2263, Ahmadu Bello University campus, Zaria B.M. 1967.2239–44, Siberia, A.B. University campus Zaria B.M. 1967.2254–7, Old City, Zaria B.M. 1967.2245–7, B.M. 1967.2258–61, Mile 5, Zaria Road B.M. 1967.2248–52, B.M. 1967.2253, Zaria B.M. 1967.2262, Near Oomawa, at foot of Kwatarakwashi rock B.M. 1968.490–495; *Plateau Prov.*, Jos B.M. 1968.486–487, Hillcrest School, Jos B.M. 1968.488.

REMARKS. The whereabouts of four of the type specimens of *Agama a. benueensis* (959, 1372, 1441 and 955) listed by Monard (1951) are not known at present. Thys van den Audenaerde tells me he believes that part of the Monard material originally lodged in the herpetological collection at La Chaux de Fonds was transferred to other European institutions and that the missing Cameroun agamas may have been among it. The thirteen individuals from the *benueensis* type series that are available and have been re-examined belong to two morphologically very different forms, and as referred to in the introduction to this paper, the name *benueensis* is applied to the blue-throated form. The other form is described as *A. paragama* sp. n. The Monard specimens here assigned to *A. benueensis* are those males from the Upper Benue that are described by him (1951) as having " une tache noirâtre à la gorge ", " une tache foncée à la gorge " and " une raie vertebrale claire ", as well as four females and a juvenile male that have a feebly developed pattern characteristic of immature and female Nigerian *benueensis*, and two males from Tibati, Adamaoua Plateau which he assigned to *A. agama boensis*. The Tibati males, M.H.N.C.F. 673, 784, have been examined by Dr. Braestrup who reports (in litt.) that both individuals have chin as well as gular spots. The presence of the gular spots, even if faint, identifies them as *benueensis* for this species is the only West African agama that has a bilobed blotch in this region in the adult male. In the Tibati males the midbody count is about 74, the vertebral counts 45 and 47 which accord with Cameroun examples of *benueensis*. Neither I nor Dr. Braestrup has seen the female, M.H.N.C.F. 726, which Monard also referred to *A. a. boensis* and its identification remains in doubt.

DIAGNOSIS. A large sized *Agama* (body length of ♂ up to 113·0 mm., of ♀ to 74·0 mm.) related to *A. sankaranica* and characterized by a high average number of midbody scale rows, 74–98 (M 88 : N 71) in Nigerian populations, ventrally directed temporal scales and marked sexual dimorphism. Dorsal trunk scales each with one to three single "hair-bearing" scale organs close to base of mucrone, nostril below canthal ridge; in these respects similar to *A. sankaranica*.

DESCRIPTION OF LECTOTYPE M.H.N.C.F. 961, ♂. Body subcylindrical, little depressed above, 3·7 times the head length. Nostril below a line connecting the canthal-supraciliaries with the rostral-labial suture, its aperture round, situated in the posterior third of an elongated, pear-shaped nasal, directed superior-laterally. From the upper rim of the nostril to the front of the nasal shield is a distinct ridge. Canthal-supraciliaries 8 : 9, the anterior forming broad sutures with the nasals at their posterior borders. Supraorbitals quite smooth, supratemporals distinctly keeled, temporals only very slightly keeled. The scales overlying the supratemporal arcade and the postorbital bone directed forwards and slightly upwards; ventrally the imbrication of the scales covering the posterior part of the jugal, the broad portion behind and below the eye, as well as those over the temporal fossa directed downwards and slightly backwards; no row of keeled juxtaposed scales. Occipital plate enlarged, broadly oval, its length equivalent to the horizontal diameter of the tympanum. Seven to ten upper labials, eight to twelve lower labials. Tufts of enlarged, conical, rather flat scales around the ear, one, consisting of three scales, on the anterior border, one on the upper posterior border, on the lower posterior border a group of about four to five more prominent conical scales and below this group a curved *row* of about five flattish conical scales. At the side of the neck midway between the tympanum and a shallow neck pit, but a little above, a rosette of spines, the longest scale in the rosette two-thirds the length of the nasal. Behind and a little below this rosette and situated above the neck pit an oblique or vertical line of conical scales. Above and slightly behind the tympanum a prominent erect scale surrounded by a few lower but erect scales. Ear subtriangular, its horizontal diameter equal to the distance from the tip of the snout to the middle of the nasal. A gular pouch present. Nuchal crest low, formed from about ten conical scales; no dorsal nor caudal crest. Dorsal scales imbricate, homogeneous, strongly converging on the vertebral line, strongly keeled but the keel not markedly compressed, mucrone finely tapering, ventrals and subcaudals smooth.

A maximum of two scale organs on each body scale but usually only one and situated under the dorsodistal edge of the scale close to the base of the mucrone. Each scale organ bears a single " hair ".

Midbody scale count 78; vertebral count 46; preanal pores in two transverse rows, 13 anteriorly, 15 posteriorly. The adpressed hind limb reaches to posterior border of the tympanum. Nineteen lamellae under the fourth toe. First toe three or four lamellae shorter than fifth toe, third toe one lamella shorter than fourth toe.

Tail slightly depressed at the base; broken. Caudal scales keeled and mucronate, arranged in distinct whorls.

Body size 94·0 mm.

COLOUR IN ALCOHOL. Apart from a conspicuous whitish vertebral line approximately three scales wide and extending from the nape to the base of the tail there is little colour pattern discernible. Any pattern that may have been present on the flanks of the living animal has become obscured by preservation and sloughing and only a slight mottling of cream and dark brown is now evident. The throat bears a large, blackish, bilobed patch at the level of the gular fold; in front of this patch and extending on to the chin are several small, dark spots on a cream background. The rest of the undersurfaces are a grey-cream.

COLOUR IN LIFE OF NIGERIAN EXAMPLES. Dorsum grey or brown with whitish dark-edged ocelli on the flanks which are arranged in two or three longitudinal rows, the spots in the outer, or middle in the case of individuals with three rows on each side, generally larger than the others. Across the back from the shoulders to the tail a series of dark chocolate brown bands which, particularly in juveniles, are considerably broader and often diamond-shaped on the vertebral line and enclose a narrow, longitudinal, whitish streak. The streaks become confluent in some adult males and females (see sex dimorphism) and form a diffuse yellowish vertebral stripe. Schiøtz (personal communication) describes the entire dorsum and belly of adult males as having a distinct bluish tinge, but not of such an intense blue as the *Agama agama* dominant male, while the chin and throat are yellow with two to four dark blue or black patches. The upper surface of the male's head is irregularly mottled green; the tail is greenish with indistinct yellow bands.

The ground colour of the female varies according to the colour of the rocks or soil in its habitat. At maturity the transverse bands on the trunk are reddish brown and the sides of the head are greenish. The ventral surface of both the female and the juvenile is white but the chin and gular region of most individuals has a network of dark lines forming irregular spots.

INTRASPECIFIC VARIATION. An analysis of meristic variation in the material examined shows some geographical differences. The samples from the western region (Igbetti and Idanre) have the highest midbody and vertebral counts, midbody 84–98 (M 91·3 : N 34), those from the Jos Plateau and the Cameroun the lowest, 68–82 (M 76 : N 11) while the gradation in the Zaria Province population almost spans these two extremes, 74–96 (M 85·8 : N 34). The variation in these characters for the entire series is : midbody 68–98 (M 87·0 : N 79), vertebral 41–56 (M 48 6 : N 76). The correctness of the identification of the individuals at the extremes of the variation is not in doubt, a combination of other characters such as throat markings, position of nostril, trunk scale organs and direction of imbrication of the post-orbital/temporal scales assigning them unquestionably to *benueensis*. Variation in the number of fourth toe lamellae (nineteen to twenty-three) and in the relative lengths of the first and fifth, and third and fourth toes is independent of the variation observed in midbody and vertebral counts and appears to have no geographical nor ontogenetic significance. The third toe may equal the fourth but generally it is shorter by half to one lamella. Variation in the relative lengths of the first and fifth toes is greater; the first is always shorter than the fifth but the difference may be as many as four lamellae.

In the majority of the examples studied the lateral head scales between the eye and the ear all imbricate downwards or downwards and slightly backwards but in a few individuals, juveniles as well as adults, the scales in the lower posterior quarter of this area, that is those overlying the temporal fossa are directed forwards and upwards, in other words in a similar direction to those of *Agama agama*; however they are not as strongly keeled as in *agama* nor are they separated from the post-orbital/supratemporal scales by an oblique row of juxtaposed scales.

Scales on either side of the nuchal crest are not or only slightly mucronate and are only slightly keeled. They are considerably larger than the scales below the central group of spines on the side of the neck.

SEXUAL DIMORPHISM AND DICHROMATISM. Some sexual dichromatism is evident, notably in the conspicuous gular and chin spots which are a characteristic feature of the adult male. The twin gular spots develop before the chin spots and first appear as a darkening of the median gular region which later becomes an intense black or navy bilobed blotch; occasionally the lobes are separated on the midline.

The gular spots do not develop until the male reaches a body size of over 73 mm., although there is one exception among the fifty-six males examined, a 69·7 mm. individual collected at Igbetti. By 80 mm. most of the males have developed two additional dark spots; these are on the chin and somewhat oval and parallel to each other on either side of the median line. The development of these gular and chin spots in adult male *benueensis* does not seem to be seasonal; they are present in Nigerian individuals collected in January, February, March, June, July and August. The three largest males in the Cameroun series (72·5, 78·3 and 74·0 mm.) which were obtained in July and in September have only gular spots.

Adult males retain some evidence of the juvenile pattern; generally the two longitudinal rows of ocelli along each flank are discernible, although feebly, as well as remnants of the five dark transverse lines in the mid dorsal region on each side of the midline from shoulders to groin but the light coloured vertebral streaks, a characteristic feature of the juvenile livery, invariably coalesce and form an ill defined light vertebral zone extending from the nape to the tail. The female sample is insufficient to be certain whether a similar light vertebral zone always develops at maturity. Only six of the fifteen females are gravid and of these six only the two Cameroun examples (M.N.H.C.F. 1460, 1269) have a clearly defined continuous light line. In the other examples the vertebral pattern is obscure in all but one of the Igbetti examples (Z.M.C. 36351). In both sexes the dorsolateral series of ocelli becomes progressively less distinct as the individuals mature. Egg bearing females were obtained in July, August and September. Preanal pores are usually ten to twelve in a single series but in three Idanre males, the only male *benueensis* collected there, and in the lectotype the pores are in double series 13 + 14, 10 + 13, 8 + 13, 13 + 15 respectively.

ECOLOGY. In the western region of Nigeria Schiøtz (personal communication) says that *A. benueensis* is strictly confined to large rocky outcrops such as the vast gneiss inselbergs where it is common both in the savanna (Igbetti) and in the forest (Idanre). Other ecological niches that he searched in southern Nigeria, such as mounds of boulders, small rocky areas, produced no examples. He noted that *benueensis* hides in rock crevices and among vegetation at the perimeter of an inselberg but conducts its feeding and sexual activities on the actual surface of the rock. Farther north on the Jos Plateau the species is much less abundant but it is again quite common in Zaria Province on the inselbergs around Zaria City as well as in a variety of other habitats such as on mounds of laterite on open farmland in the Galma Fadama, a locality some miles from the nearest inselbergs, on sandy river banks (Amethyst River) and in sandy stream beds (R. B. Walker, personal communication). Near Sabon Gari, in an area of scrap cars and garbage tips, both *A. benueensis* and *A. agama* were taken and no specific habitat preference was noted but Schiøtz maintains that at Igbetti *A. benueensis*, *A. sankaranica* and *A. agama* can be seen virtually only a few feet from each other yet each still adhering to its preferred habitat.

A careful search by Schiøtz of the Shai Hills in Ghana and suitable localities in the Eastern Region of Nigeria failed to produce any *benueensis* and he believes the species may also be absent from the Bamenda region of the Cameroun. *Agama benueensis* seems to be endemic to the Western and Northern regions of Nigeria and the upper Benue valley in the Cameroun.

Monard (1951) does not record the biotopes for the type series of *benueensis* and he describes only the general areas around the villages. The 1 : 1,000,000 maps of the Upper Benue show the villages where *benueensis* were taken as being in an area deeply dissected by the Benue and its tributaries and at altitudes varying from 740 ft. to 1,400 ft.; only Ngaouyanga is on a high steep-sided wooded platform, the other localities are in or at the sides of valleys in woodland savannah.

RANGE. West Africa: Western and Northern Regions of Nigeria and northern Cameroun.

Agama sankaranica Chabanaud

(Pl. 3, figs. a, b; Pls. 4, 5)

Agama sankaranica Chabanaud 1918 : 105.
Agama boensis Monard 1940 : 155 (part: adults only).

MATERIAL EXAMINED. PORTUGUESE GUINEA, Madina Boé M.H.N.C.F. 865, 867–8 (three of the syntypes of *Agama boensis*). REPUBLIC OF GUINEA, Beyla M.N.H.N. 21.309–316, Kankan M.N.H.N. 21.297–298, Kerouané M.N.H.N. 21.299–308, B.M. 1921.11.12.1–5. MALI, Moussaia, Sankaran M.N.H.N. 1901.395 (holotype of *Agama sankaranica*). GHANA, B.M. 1930.6.9.8 Korley Bu, Accra B.M. 1931.5.6.3, B.M. 1932.6.1.5–7, Tamale B.M. 1927.9.27.199, Tafo B.M. 1962.910. NIGERIA, *Benue Prov.*, Makurdi B.M. 1937.12.4.14; *Plateau Prov.*, Shendam B.M. 1962.1573; *Kano Prov.*, Kano B.M. 1961.2069, B.M. 1962.567 (no. 567 later skeletonized); *Zaria Prov.*, B.M. 1967.2206, Rimi, South-east of Kaduna B.M. 1962.1572, Zonkwa B.M. 1962.1571, Ahmadu Bello University campus, Zaria B.M. 1967.2205, 14 miles South of Zaria B.M. 1967.2204; *Lagos Prov.*, Lagos B.M. 1960.1.7.28; *Oyo Prov.*, Igbetti Z.M.C. R 36386, 36388, 36390, 36393, 36395–6, 36398, 36403, 36405, 36407, 36597, 36607, 36697–8, 36691, 36758.

DIAGNOSIS. A medium sized *Agama* (body length of adult males averaging 66 mm., of mature females 76 mm.) belonging to the group of agamas that have the nostril below the canthal ridge, homogeneous scaling and dermal sense organs not exceeding three in number on each trunk scale. Related to *Agama benueensis* Monard but distinguished by a lower average midbody count (69·6) and by dorsally directed temporal scales.

DESCRIPTION. Body subcylindrical, scarcely depressed above, 3–3·7 times the head length. Nostril below the canthal edge, situated in the posterior half of a slightly swollen, oval nasal, directed laterally. No post nasal separating the first canthal supraciliary from the nasal. Scales of the head keeled; the interorbital scales considerably smaller than the supraorbitals; imbrication of temporals directed upwards and of supratemporals directed upwards and forwards (Pl. 3 fig. b) Occipital large, its greatest width equivalent to or as much as one and a half times greater than the diameter of the tympanum. Eight to twelve upper labials; a similar number of lower labials. Usually three tufts of long, conical spines on posterior border of ear; behind and above these a single group of spines and yet farther back and just above a shallow neck pit another group of somewhat shorter spines. A weakly developed gular pouch. A low nuchal but no dorsal or caudal crest. Dorsal scales homogeneous, broadly rounded, strongly keeled and mucronate, the sharp high keel extending the length of each scale, the mucrone very slender. Scales on the flanks slightly smaller than dorsals, similarly keeled and mucronate. Ventrals keeled only in juveniles. " Hair-bearing " sensory pits on the dorsal midtrunk scales confined to around the base of the mucrones, at or just under the dorsodistal edges of the scales. The maximum number of scale organs on each scale is three but invariably no more than two are present. In the vertebral region at midbody there are generally two " hair-bearing " pits, each with a single hair-like projection, the one pit close to the base of the mucrone or under the mucrone and concealed in dorsal view, the other on the opposite side of the mucrone but near the apex of the scale. On more lateral scales there is a tendency for only the more lateral, that is lateral with respect to the mucrone, to develop.

The number and position of the scale organs on the dorsal scales bear a close similarity to the condition obtaining in East African *rueppelli* and described and figured by Scortecci (1937). Midbody scale count 64–78 (M 69·6 : N 61); vertebral count 32–46 (M 38·8 : N 61). Mature males with eight to twelve usually ten preanal pores in a single transverse row. Fifteen to twenty-one lamellae under the fourth toe. First and fifth toes subequal or first toe one lamella shorter. Third toe usually subequal to fourth toe, rarely half to one lamella shorter or longer than fourth. Tail one and three quarter times the body length, depressed at the base, slender and cylindrical distally, its scales strongly keeled and very distinctly mucronate, not arranged in distinct whorls.

Colour in alcohol. Upper parts reddish brown. Invariably a conspicuous yellowish or russet vertebral stripe from behind the head to the proximal third of the tail, much broader and always prominent in the cervical region but narrowing rapidly to a width of approximately two scales on the rest of the body. On each side of this stripe and from nape to tail broad, dark brown, transverse bands, six between the nape and hind limbs. At the lateral extremities of these bands light-coloured ocelli or elongated blotches which in some specimens coalesce to form a light dorsolateral stripe. In some examples the vertebral stripe widens at the level of each transverse band to form light diamond-shaped areas. Halfgrown individuals occasionally have indistinct marbling on the flanks below the ocelli or dorsolateral stripe. In one mature male, collected at Zaria, the transverse bands are broken up into irregularly shaped blotches. Between the eyes a thin dark transverse line is present; four similar lines radiating from the eyes to the lips are usually evident. Limbs indistinctly cross-barred with narrow dark lines.

Sexual Dimorphism. There are no obvious external differences between the females and immature males. Adult males have eight to twelve preanal pores and also broken, longitudinal, blue stripes on the chin and throat which become more prominent with maturity and often enclose a large, dark blue, median gular spot and a lozenge-shaped chin blotch. The rosettes of neck spines and the lips may also be blue in mature males. Adult females are on average rather larger than adult males. The body length of mature females varies from 68–85 mm. (average 76·2 mm.) while males vary from 62–76 mm. (average 66·4 mm.).

REMARKS. The examined material consists of examples from throughout the known range of the species. No evidence of geographical variation can be demonstrated. The examples from the extreme west of the geographical range of *sankaranica* are the three adults, two males and one female, in the series of syntypes of *Agama boensis* Monard. These individuals unquestionably belong to *sankaranica*. The throats of the males have the blue blotches and stripes that are typical of mature male *sankaranica*, furthermore the scale counts and other morphological characters including the density and distribution of trunk receptors agree well with *sankaranica* although one male with a midbody count of 64 is exceptional in having 20 : 21 lamellae under the fourth toe, which is outside the range for all other specimens examined (fifteen to nineteen). The fourth syntype of *boensis*, a juvenile, lacks a nuchal crest and clusters of neck spines and has a single apical scale organ on each body scale; it is conspecific with *Agama weidholzi* Wettstein. (Grandison, in press.) The Cameroun individuals assigned by Monard (1951) to *A. a. boensis* are discussed in the section on *A. benueensis*.

ECOLOGY. In the field this species has often been confused with female and immature *Agama benueensis* and as a result some ecological information claimed to be on *A. sankaranica* has had to be disregarded or treated with suspicion in this study. Dr. Arne Schiøtz' reliable field notes and comments make it clear that he readily distinguishes *sankaranica* from *benueensis* and his notes correspond with my own field observations in stating that unlike all other Nigerian species of Agama, with the exception of *gracilimembris*, *sankaranica* does not form family groups but is a solitary creature. The species has been observed and captured in ploughed farmland and in maize and cassava plantations when running along the rutted ground, also on paths in grass covered savanna. Schiøtz' notes state that he saw the species on the ground only in grass covered savanna or in rather dense tree savanna and never in forest nor on rocks. The localities at which examples of *A. sankaranica* have been collected are, with one exception, in the Doka and True Guinea woodland belts from Nigeria westwards to Portuguese Guinea; the exception is an individual taken at Kano which is towards the southern limit of Sudan woodland.

RANGE. West Africa: Portuguese Guinea to Nigeria.

Agama gracilimembris Chabanaud

(Pl. 3, figs. c, d; Pl. 6)

Agama gracilimembris Chabanaud, 1918 : 106.

MATERIAL EXAMINED. DAHOMEY, M.N.H.N. 04.114–5 (syntypes). NIGERIA, *Benue Prov.*, Lafia B.M. 1938.3.1.47, Wukari B.M. 1938.3.1.48–9; *Plateau Prov.*, Shendam B.M. 1962.1570; *Zaria Prov.*, Zonkwa B.M. 1961.949, B.M. 1962.1569, Samaru Bush, Zaria (on exchange to Vienna Mus.); *Oyo Prov.*, Igbetti Z.M.C. R 36654, R 36701, R 36263; *Kano Prov.*, Kano B.M. 1961.2067–8, B.M. 1962.566, CENTRAL

African Rep., " Pays des Senoussi " M.N.H.N. 17.191 (according to information received from Dr. J. Guibé this specimen was collected in the neighbourhood of Ndellé, 8° 25′ N : 20° 36′ E).

Diagnosis. A small sized *Agama* (body length of males up to 47 mm., of females to 57 mm.) lacking tufts of erect spiny scales behind the ear and bearing only one receptor on each body scale, related to *Agama weidholzi* Wettstein but distinguished by heterogeneous body scales, strongly keeled head scales and a low fourth toe lamellar count (13–14).

Description. Body slightly depressed, 3–3·6 times the head length. Nostril below the canthal edge, situated in the posterior half of a convex, often keeled, oval or pear-shaped nasal; directed laterally. Interorbital scales as large or larger than the supraorbitals. Above the nasal a continuous series of three clearly defined, somewhat elongated scales runs from the rostral to the canthal-supraciliaries. The first canthal-supraciliary is separated from the nasal by a small postnasal. Scales of the head strongly keeled, somewhat rugose; imbrication of temporal scales directed downwards and slightly backwards. Occipital large, its greatest width equivalent to the diameter of the tympanum. Nine to twelve, usually ten upper labials; eight to eleven, usually ten lower labials. No tufts of spines around the ear, instead single, short, conical scales close to the border of the ear and three to four tubercles on the side of the neck in a slightly curved row extending from the upper edge of the ear to above a point midway between the neck pit and the arm insertion; additional tubercles irregularly scattered below this row and between the ear and the neck pit, the lowest at the jaw angle. No gular fold. No trace of a nuchal or dorsal crest. Dorsal scales heterogeneous, those in the vertebral region a little larger than the lateral series; on the flanks, and irregularly disposed, some large scales which are as big and occasionally bigger than the vertebrals.

The scales of the midtrunk region broadly oval or pear-shaped with pronounced " shoulders ", dorso ventrally flattened on each side of a high keel, the edges of which rise abruptly from the scale. The keel extends half to two-thirds the length of the scale but does not project beyond the scale apex to form a mucrone. A single sensory organ is present on the dorsodistal surface of each of the midbody scales just under the keel tip or very slightly to one side and sometimes evident only when the scale is viewed from behind. Generally each of these organs bears one but never more than one " hair ", which projects slightly beyond the apex of the scale and by macroscopic inspection may be mistaken for a mucrone. Gular and ventral scales strongly keeled. Midbody scale count 70–85 (M 74·8 : N 16) vertebral count 30–46 (M 37 : N 15). Mature males with eight to twelve preanal pores in a single transverse row. The adpressed hind limb reaches to the tympanum. Thirteen to fourteen lamellae under the fourth toe. The first toe is usually either one lamella longer than the fifth toe or equal to it; rarely (two examples) is it shorter (half lamella). The third toe exceeds the fourth toe in length by half to two lamella. Tail one and a half times the body length, depressed at the base, slender and cylindrical distally its scales strongly keeled and slightly mucronate, and not arranged in whorls.

Body length of gravid females 49·0–56·7 mm., of mature males 44·0–47·0 mm.

Comparison of characters of Nigerian species of *Agama*

	*agama**	*paragama**	*benueensis**	*sankaranica*	*gracilimembris*
Dorsal body scales	Homogeneous	Homogeneous	Homogeneous	Homogeneous	Heterogeneous
Position of nostril	On canthus	On canthus	Below canthus	Below canthus	Below canthus
Dorsal body scales keeled and mucronate	+	+ (strongly)	+	+ (strongly)	Keeled but not mucronate
Keeled ventrals	—	—	—	+ (juveniles only)	+
Midbody count	59–77 (M68·2 ♀ : M66·2 ♂)	50–66 (M58·5)	74–98 (M91·3 W.R.: M85·8 Zaria)	64–78 (M69·6)	70–85 (M74·8)
Vertebral count	38–55 (M46)	26–34 (M30)	42–56 (M50)	32–46 (M39)	30–46 (M37)
Nuchal crest	+	+	+	+	—
Imbrication of scales in temporal region on left side of head	↘ ↖	↘ ↖	↘ (rarely ↘) ↖	↖	↘
Number of receptors per dorsal scale	1–8	3–9	1–2 (rarely 3)	1–2 (rarely 3)	1
Keeling of dorsal head scales	Faint	Faint	Faint	Keeled	Strongly keeled
Fourth toe lamellae	18–25	17–21	18–23	15–21	13–14
First to fifth toe (difference expressed in number of lamellae)	<(3–6)	<(3–5)	<(3–4)	Subequal	<(½), = or >(1)
Third to fourth toe	= or <(1–3)	<(½–2)	= or <(½–1)	= or <(1) or >(1)	>(1–2)
Body length of gravid ♀	84–91 mm.	96–107 mm.	65–74 mm.	68–85 mm.	49–57 mm.
Body length of adult ♂	107–137 mm.	99–108 mm.	80–113 mm.	62–76 mm.	44–47 mm.
Tufts of spines behind ear and on side of neck	+	+	+	+	—

* Based on Nigerian individuals only.

Colour in alcohol. ♂ Upper surfaces of body and limbs greyish brown; usually a clearly defined light vertebral stripe which extends from behind the occiput to the base of the tail. Straddling the vertebral stripe from nape to base of tail are nine ‹› shaped, dark chocolate brown marks which in some specimens are rather obscure. Iu the same region and alternating with these marks, diamond-shaped brick orange zones occasionally present. The lips, snout, supraorbital and tympanic and parietal regions invariably dark brown or blue black but a lighter area over the occipital is always present. Dark, irregular, longitudinal lines are usually present on the throat, chest and belly but they may extend no farther backwards than the gular region. In a sexually mature male these lines are dark brown and closely set to give a brownish appearance to the entire belly; the throat has a dark median area.

♀ The entire dorsal surfaces of the body, tail and limbs brown with obscure, irregularly placed lighter areas. An ill defined light vertebral stripe occasionally present. Snout, supra-orbital area, cheeks and olbique stripe from below eye to commissure of lips dark brown; occipital, temporal and nuchal regions light fawn. Above and behind each ear a large ill defined blackish patch in which the small pointed scales stand out clearly as light bluish or greyish spots. Lower surfaces greyish white with faint longitudinal dark lines from throat to belly. In some specimens these lines do not extend farther than the chest.

Ecology. *A. gracilimembris* is the rarest of the West African savannah species and has been recorded from only a few localities all of which are in the Doka and True Guinea woodland vegetation belts and on the extreme southern limit of Sudan woodland (at Kano). Its biotope has not been described.

Range. West Africa: Dahomey to Ubangi Chari.

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Summary of taxonomic changes:

Agama boensis Monard part = *A. sankaranica* Chabanaud
Agama boensis Monard part (juvenile) = *A. weidholzi* Wettstein
Agama a. benueensis Monard part = *A. benueensis* Monard
Agama a. benueensis Monard part = *A. paragama* sp. n.

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PLATE 1

a. *Agama paragama* sp. n. Holotype B.M. 1967.2215.
b. *Agama paragama* sp. n. Lateral view of the head of the holotype.
c. *Agama agama* L. Lateral view of the head of a juvenile female B.M. 1967.2212.
d. *Agama agama* L. Dorsal view of same individual.

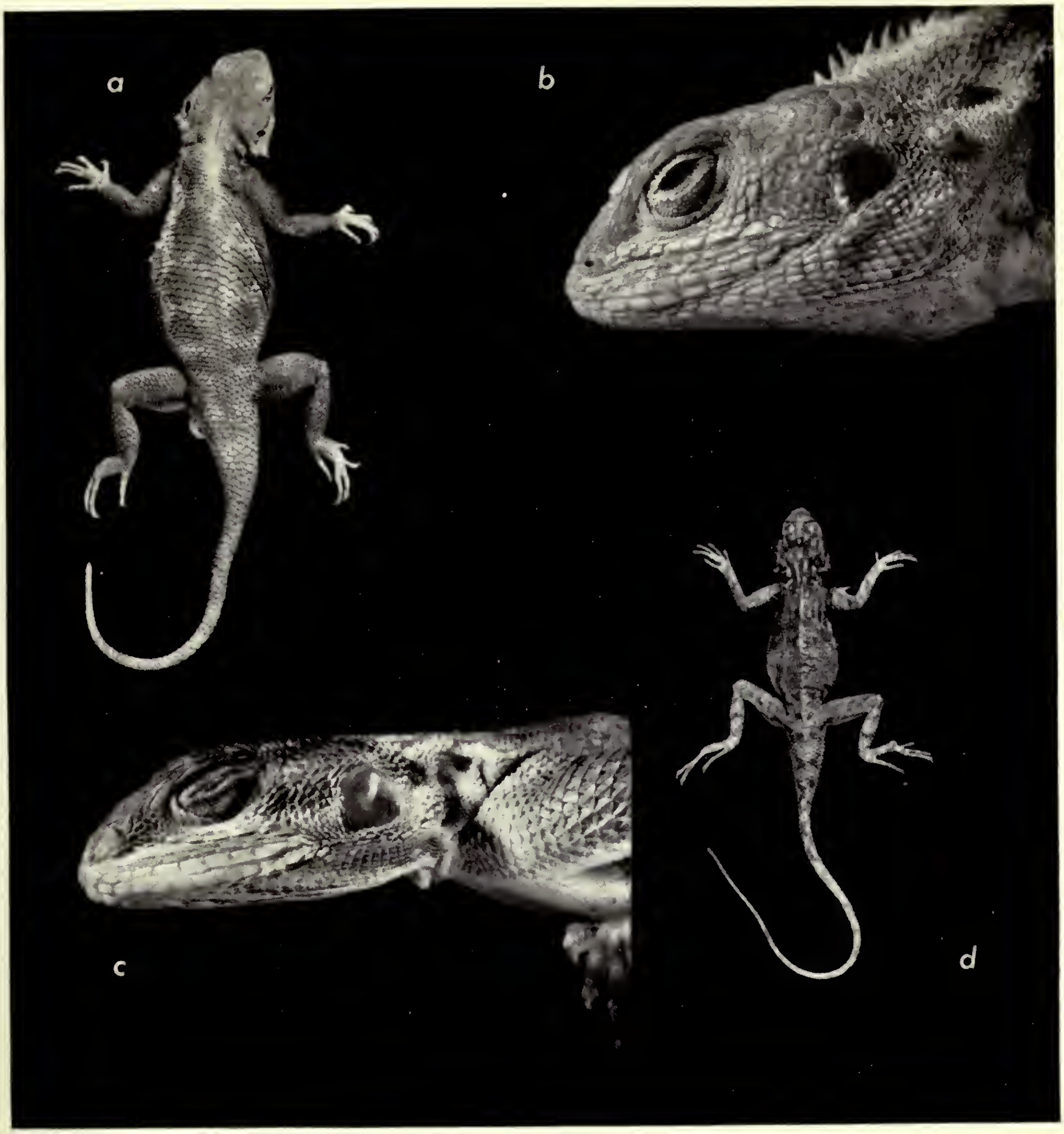
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PLATE 2

a. *Agama benueensis* Monard. Dorsal view of an immature male B.M. 1967.2239.
b. *Agama benueensis* Monard. Dorsal view of an adult male B.M. 1967.2234.
c. *Agama benueensis* Monard. Throat of a sexually mature male B.M. 1967.2253.
d. *Agama benueensis* Monard. Laterial view of the head of an immature male B.M. 1967.2239. Note developing dark gular patch.

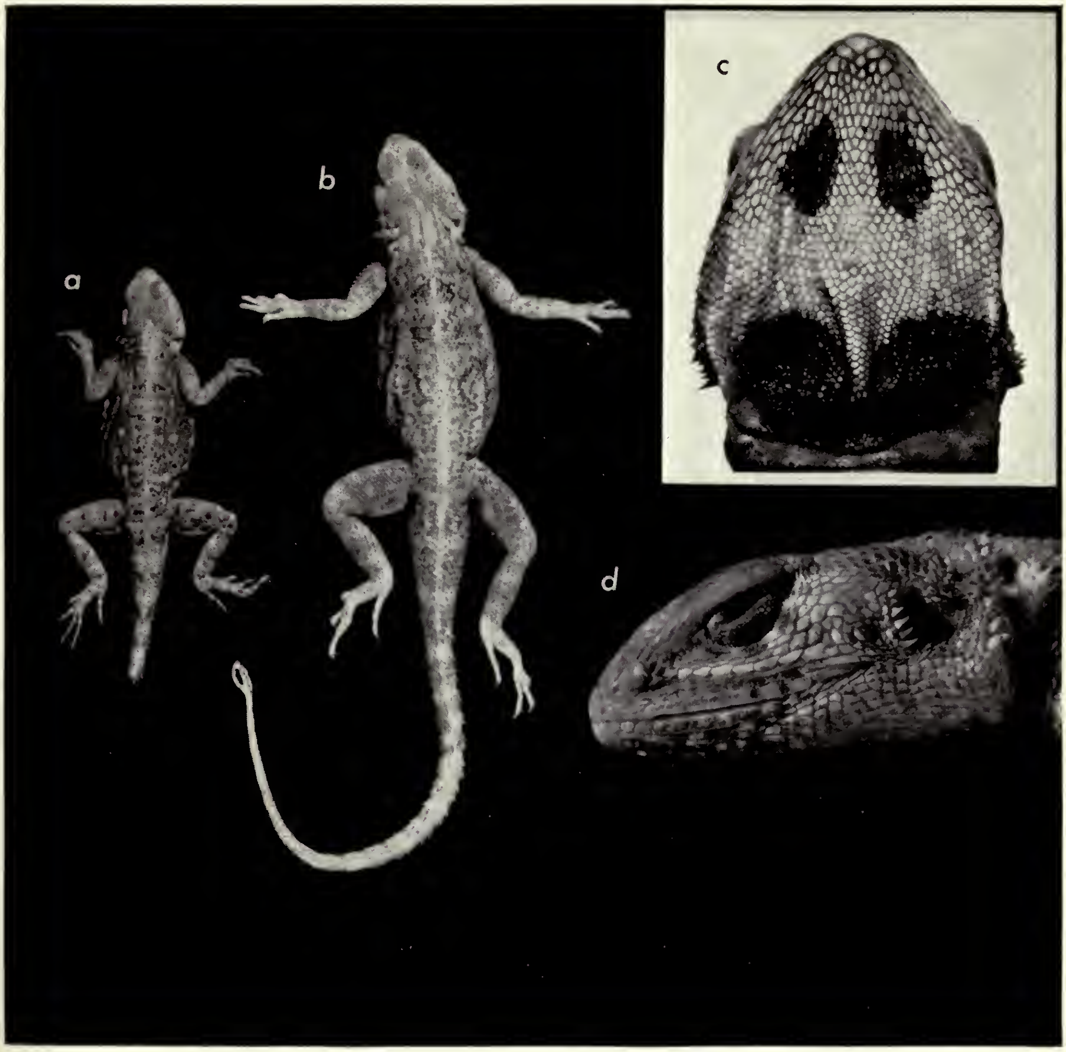
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PLATE 3

a. *Agama sankaranica* Chabanaud. Dorsal view of an adult female B.M. 1967.2204.
b. *Agama sankaranica* Chabanaud. Lateral view of the head of the same individual.
c. *Agama gracilimembris* Chabanaud. Lateral view of the head of an adult male B.M. 1961.949.
d. *Agama gracilimembris* Chabanaud. Dorsal view of same individual.

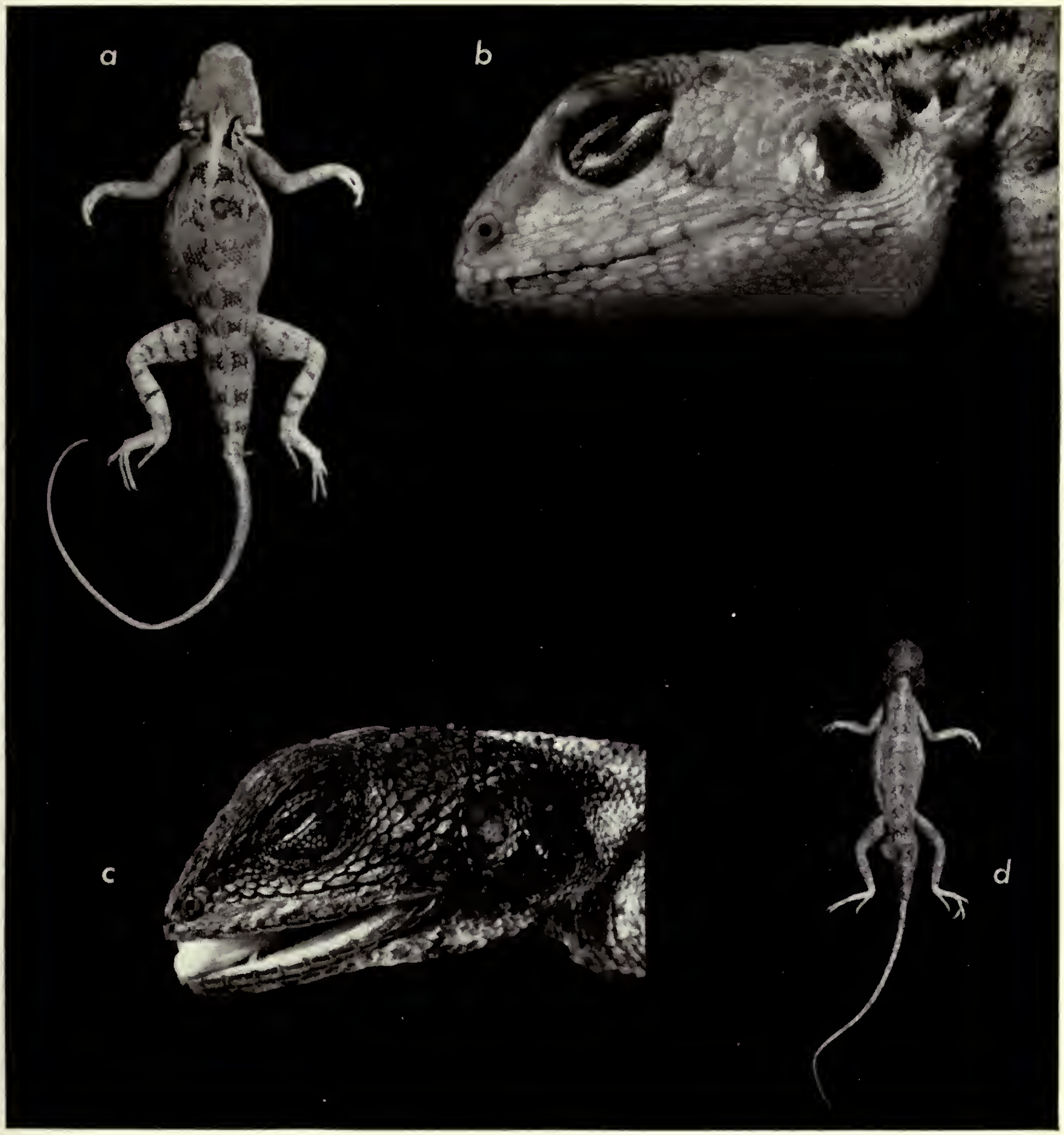
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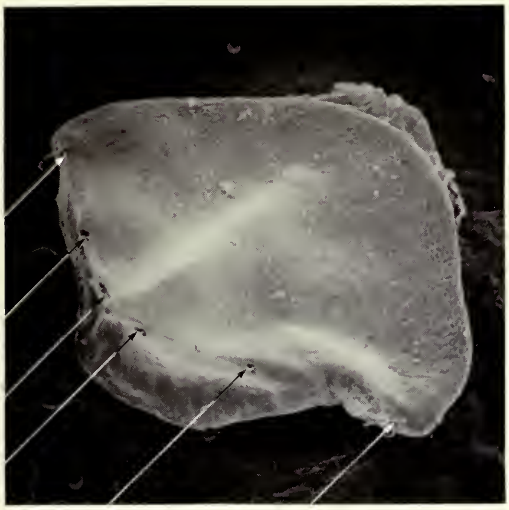
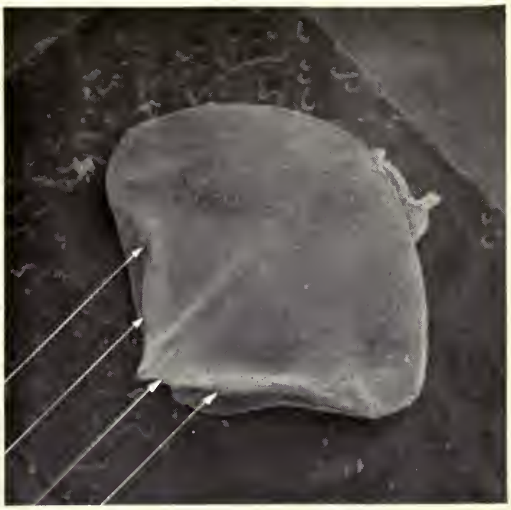
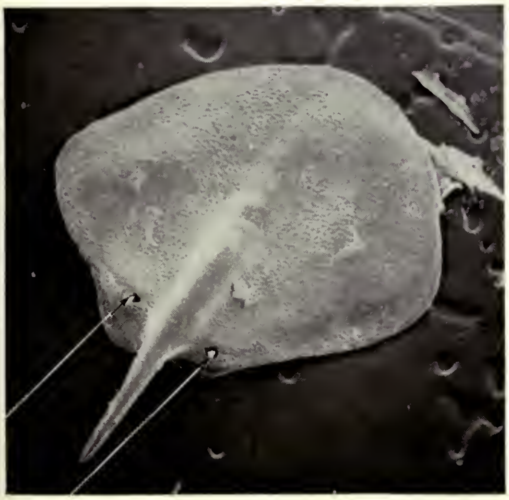
PLATE 4

Stereoscan electron microscope photographs of dorsal midbody scales. Arrows point to the sense organs.

Upper row left to right.	*Agama agama*	B.M. 1962.1595 × 48
	Agama paragama sp. n.	Holotype × 28
Lower row left to right.	*Agama benueensis*	B.M. 1967.49 × 52
	Agama sankaranica	B.M. 1967.2204 × 47







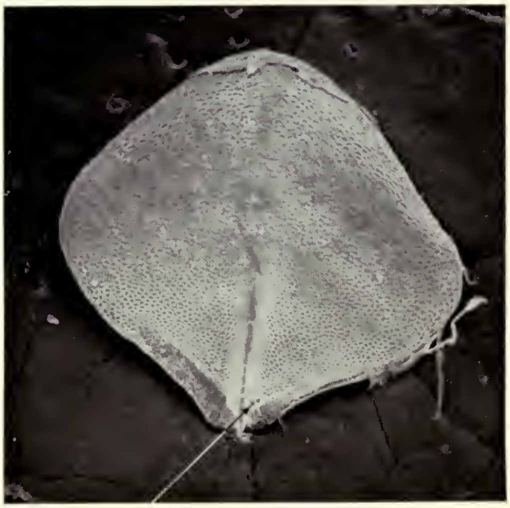
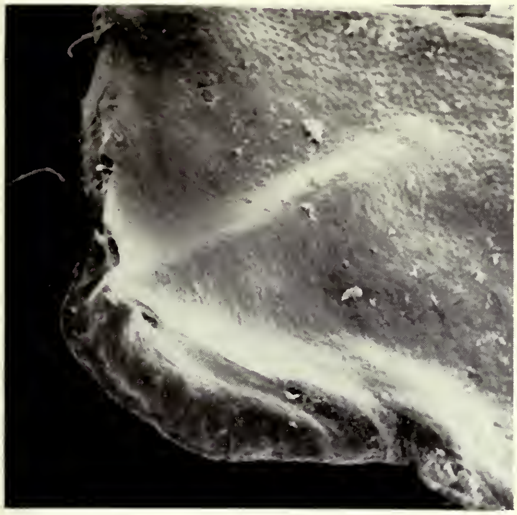
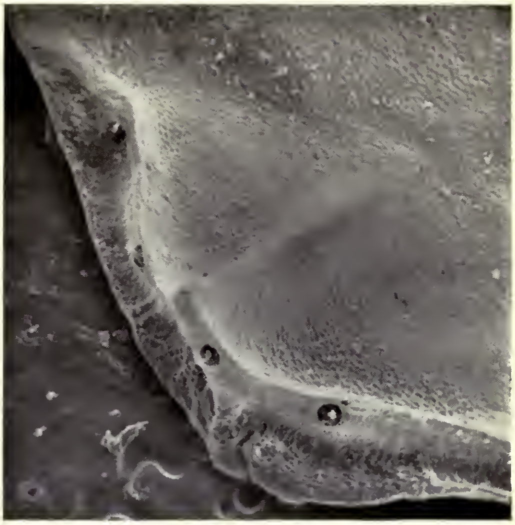


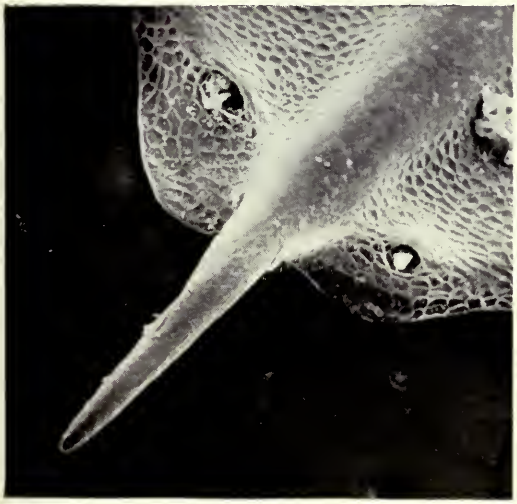
PLATE 5

Stereoscan electron microscope photographs of the apices of the same trunk scales as illustrated in Plate 4 showing the positions of the sense organs relative to the keel and dorsodistal margin and the single " hair " protruding from each receptor.

Upper row left to right.	*Agama agama* × 70 *Agama paragama* × 70
Lower row left to right.	*Agama benueensis* × 131 *Agama sankaranica* × 260







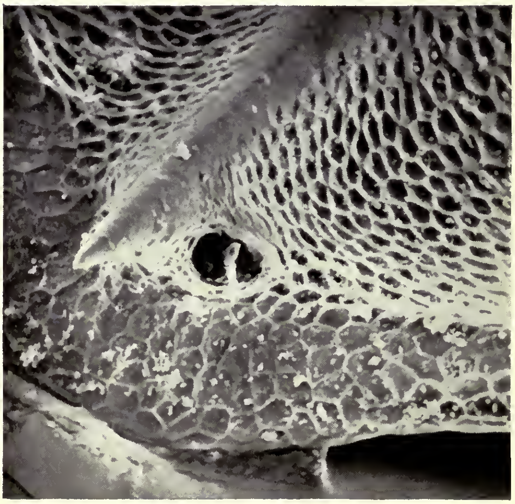
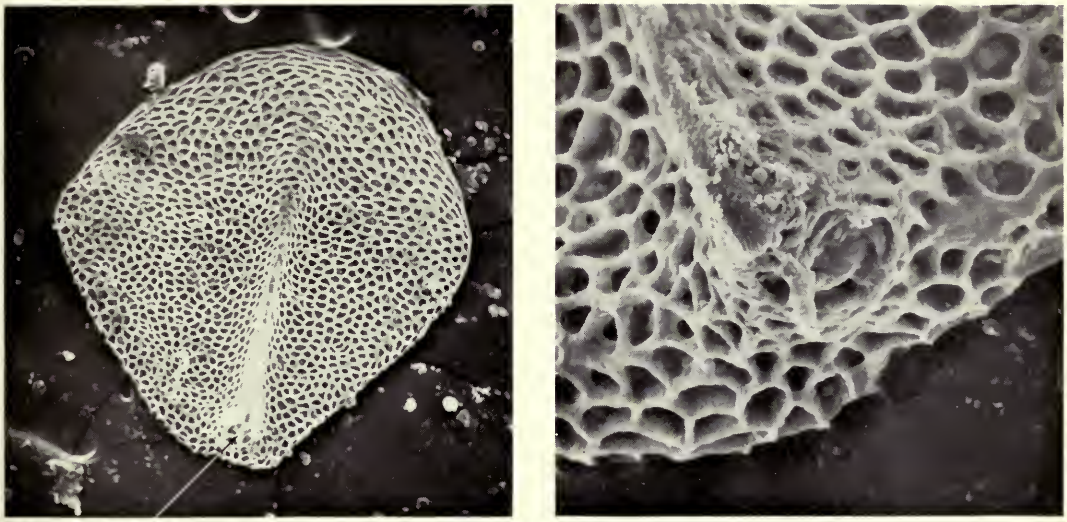


PLATE 6

Stereoscan electron microscope photographs of a dorsal midbody scale of *Agama gracilimembris* B.M. 1961.949 showing the position of the single " hair-bearing " sense organ directly below the termination of the keel.

Left × 110. Right × 580.



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A REVISION OF THE AMPHIPOD GENUS *MICRODEUTOPUS* COSTA (GAMMARIDEA: AORIDAE)

A. A. MYERS

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Pp. 91–148; 1 *Plate,* 22 *Text-figures*

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A REVISION OF THE AMPHIPOD GENUS *MICRODEUTOPUS* COSTA (GAMMARIDEA : AORIDAE)

A. A. MYERS

SYNOPSIS

The systematic position of the Aoridae and the phylogenetic relationships of its members are discussed. All the known species of *Microdeutopus* and one new species are described and figured, with keys for their identification. The synonymy of each species of *Microdeutopus* is reviewed, and details of their ecology and distribution are given. A catalogue of material studied in the present work, and the location of type material, is given in the appendices.

INTRODUCTION

THE need for a revision of a number of genera in the Aoridae has long been indicated. Enequist (1949) pointed out that there is uncertainty about the delimitation of the species of the genera *Microdeutopus* and *Lembos*. Andersson (1954) elucidated the relationships of *Microdeutopus gryllotalpa* Costa, *M. anomalus* (Rathke) and *M. propinquus* Sars, using material collected in the Gullmarfjord and collections in the Swedish State Museum. His findings have been substantiated in the present work, which included studies on laboratory-reared material. Generally, however, field workers have experienced difficulties in the identification of aorid material, as is clear from the numbers of wrongly identified specimens that exist in many institutions. The literature is so widely scattered, and the synonymy, particularly of the European species, so confused, that a thorough revision of the synonymy and review of the literature are needed.

During the present investigations, fresh material was examined wherever possible together with preserved material from the British Museum and a number of other institutions and specimens from private donors (see Appendix 1). Laboratory reared material of *M. gryllotalpa* and *M. anomalus* was also studied.

Identification of Aoridae is frequently hindered by their fragility, specimens collected in dredge samples often being devoid of all appendages except gnathopoda, pleopoda and uropoda. Fortunately male *Microdeutopus* species can readily be identified by the structure of the gnathopoda, uropoda and telson, and by the form of the processes which arise from the peraeon segments in the mid-ventral line. These ventral processes have been shown to occur in all species of *Microdeutopus* which have been examined for this character. The only species not examined is *M. haswelli* Stebbing, which at this stage seems better not dissected since it is represented only by the single holotype specimen obtained on loan from the Australian Museum, Sydney.

In general, the structure of the mouthparts is not a valuable taxonomic criterion, except at a generic level and above, though in some species, certain minor differences can be recognized as in the structure of the mandibular processes of the paragnath in *M. schmitti* Shoemaker and *M. hancocki* Myers.

Kinne (1963a, 1963b, 1964) has shown that temperature, salinity, food, and combinations of these factors affect maximum size in some organisms. Personal observations in the laboratory (Myers, 1968d) indicate that some, if not all these factors, also affect growth rates and maximum size in *M. gryllotalpa* and presumably, therefore, in other *Microdeutopus* species. Field observations also suggest that the various species reach differing maximum sizes, in different localities, and it is therefore not possible to give an overall indication of the size at which the male of any *Microdeutopus* species reaches maturity and is hence identifiable. In particular it should be noted that high latitude specimens are generally much larger than low latitude specimens of the same species. In the systematic section the maximum recorded size, measured from the anterior margin of the cephalosome to the tip of the telson, is given for each species and each sex.

Male *Microdeutopus* are readily identifiable, and descriptions of all known species are given below, together with keys for their identification. The identification of females presents considerable difficulty, however, since aorid genera are based almost entirely upon adult male characters, of forms which show extensive sexual dimorphism. There are no characters exhibited by females which are diagnostic of the genus *Microdeutopus*. Many resemble the male in the structure of the antennules, antennae, uropoda and telson, thus exhibiting features which differ in one way or another from those of other *Microdeutopus* females, and probably from those of other female Aoridae. However, until the females of all the known Aoridae are studied, identification of solitary females within this family must remain questionable. Full descriptions and figures of ovigerous females, are given here, to aid provisional identification and also to prevent the confusion of females in samples containing more than one *Microdeutopus* species.

SYSTEMATIC POSITION OF THE AORIDAE

The Aoridae are closely related to the Photidae, from which they differ in having the first pair of gnathopoda more markedly developed than the second. *Aorcho* Barnard is intermediate in having the first and second gnathopoda of equal size and can be assigned to either family (Barnard, 1964). Also intimately related to the Aoridae are the Corophiidae, which differ from the Aoridae only in the degree of depression of the pleon. The loss of the accessory flagellum of the antennule has been described as an advanced character in Amphipoda (Barnard, 1962), and it is suggested here that the corophiid tendency towards the loss of a uropod 3 ramus is also advanced, so does not necessarily indicate close relationship between the possessors of this character. Barnard (1962) has pointed out that it has become increasingly difficult to assign, between the two families, various members of the Photidae and Corophiidae, because here too the differences involve quantitative aspects of depression or compression of the pleon. It seems probable that the family Corophiidae is polyphyletic and includes, within its framework, advanced members of both the Aoridae and Photidae. It is therefore not possible to indicate any circumscribed diagnosis for the family Aoridae, which can only be described as those members of the aorid/photid/ischyrocerid/corophiid complex which exhibit greater development of gnathopod 1 than gnathopod 2, coupled with a tendency towards retention of such primitive characters as an accessory flagellum on the antennule, uropod 3 with two rami, contiguous coxae, and no marked depression of the pleon.

The subdivision of the family Aoridae is also problematical since the complex permutations of characters among the species makes a systematic classification, based on possible phylogenetic relationships, exceedingly difficult. The accessory flagellum of the antennule exhibits a complete gradation of stages, from (a) primitively multi-articulate as in *Aora typica* Kroyer, *Microdeutopus anomalus* (Rathke), *Lembopsis spinicarpus* Pearse, *Lembos viguieri* Chevreux and others, to (b) reduced to two or three articles of which the terminal one is usually vestigial, e.g. in *Microdeutopus armatus* Chevreux, *Lemboides afer* Stebbing, and *Neomegamphopus roosevelti* Shoemaker, or microscopic as in *Aoroides columbiae* Walker. The rami of uropod 3 may be (a) more or less equally developed as in *Amphideutopus oculatus* Barnard, *Microdeutopus versiculatus* (Bate), *Lembos longipes* Lilljeborg, and *Aorcho delgadus* Barnard; (b) the endopodite may be greatly reduced as in *Acuminodeutopus heteruropus* Barnard; (c) both rami may be minute, as in *Paradryope orguion* Stebbing and *Dryopoides westwoodi* Stebbing; or (d) there may be a single ramus only as in *Neomicrodeutopus cabindae* Schellenberg. The antennae exhibit considerable variation in form. They may be (a) shorter than the antennules stout, sub-pediform, with few flagellar articles, resembling those of the Corophiidae, as in *Microdeutopus haswelli* Stebbing; (b) less stout, as in *M. gryllotalpa* Costa, *Aora typica* Kroyer, *Lembos websteri* Bate and *Lemboides afer* Stebbing; (c) slender though still shorter than the antennules, as in *Microdeutopus stationis* Della Valle, *Lembopsis spinicarpus* Pearse and *Lembos macromanus* (Shoemaker); or (d) very long and slender, exceeding the length of the antennules, with multiarticulate flagella, as in *Paradryope orguion* Stebbing and *Amphideutopus dolichocephalus* Myers. The development of median spines on the ventral surface of the peraeon segments is of frequent occurrence in the Aoridae, but such spines are not restricted to the Aoridae, being also exhibited by various members of the related family Corophiidae, including certain species of *Unciola* Say and *Grandidierella* Coutière.

Most classifications of the Aoridae have been based upon the structure of the male gnathopod 1, the gross development of which is so characteristic a feature of the Aoridae, though it is not diagnostic. Two main tendencies are discernible in this appendage: first, the great development of one or more of the articles, frequently accompanied by reduction of some of the others, and secondly, the production of toothlike processes on one or more of the articles. Classifications based on either of these characters are arbitrary, since it would be unreasonable to assume that either of these tendencies has occurred only once in the evolution of the family. Nevertheless, a good workable classification is that of Barnard (1958, 1962, 1964) which is adopted here with two important modifications suggested by present work. Firstly *Microdeutopus tridens* Schellenberg and *M. kraemmeri* Reid are transferred to the genus *Lembopsis* Pearse (see Myers 1968c); and secondly, the genus *Coremapus* Norman is incorporated in the genus *Microdeutopus* (see p. 102).

Genus *MICRODEUTOPUS* Costa 1853

Microdeutopus Costa, 1853 : 178.
Autonoe Bruzelius, 1859 (pro-parte): 23.
Stimpsonia Bate, 1862 : 162.
Microdeuteropus Norman, 1868 : 281.
Stimpsonella Della Valle, 1893 : 421.
Coremapus Norman, 1905 : 78.

TYPE SPECIES: *Microdeutopus gryllotalpa* Costa.

DIAGNOSIS. Head lobes moderately produced, obtuse; antennules longer than the antennae (with the exception of male *M. chelifer* (Bate)); article 1 of mandibular palp the shortest, article 3 the longest, article 3 broad centrally, narrowing terminally; mandibular process of paragnath acute; gnathopod 1 of male larger than gnathopod 2, complexly chelate, article 5 considerably larger than article 6; females with the first and second gnathopods dissimilar; uropod 3 with two more or less subequal rami; telson simple.

HISTORICAL. The genus was established by Costa (1853) to include the single species *M. gryllotalpa* Costa, independently described by Bruzelius under the name *Autonoe grandimana*. Bate (1856) erected the genus *Lembos* to include the species *L. cambriensis* Bate, *L. damnoniensis* Bate, *L. versiculatus* Bate and *L. websterii* Bate, but later (1862) relegated all these species to the genus *Microdeutopus* Costa (corrected from *Microdentopus* in the text, to *Microdeutopus* in the appendix). In the same year he erected the genus *Stimpsonia*, to include as monotype *chelifera* Bate, while admitting that " the genus probably bears too close a resemblance to *Microdeutopus* to be retained as generically distinct ". Della Valle (1893) noted the preoccupation of *Stimpsonia* among the Nemertina (*Stimpsonia* Girard, 1853) and erected *Stimpsonella*, including in the genus, *armatus* Chevreux with *chelifera* Bate. Norman (1868) altered *Microdeutopus* to *Microdeuteropus* for grammatical reasons but later (Norman, 1905a) reverted to the original spelling. Norman (1905b) erected the monotypic genus *Coremapus* for *versiculatus* Bate.

LITERATURE. The best general account is that of Della Valle (1893) who gives ten species. Of these, however, *M. gryllotalpa* Costa and *M. minax* Smith are synonymous, *M. tenuis* Dana is not a species of *Microdeutopus* and *M. titii* Heller is a dubious species, while the distinct species *M. versiculatus* is treated as a synonym of *M. anomalus* Rathke. The keys, which apply to males only, are adequate. Stebbing (1906) gives a good account of eight species, and not eleven as it would seem, for *M. anomalus* (Rathke) and *M. propinquus* Sars are synonymous, *M. megnae* Giles is attributable to *Grandidierella* Coutière, and the doubtful *M. titii* Heller is listed with reservation. Descriptions of the females are inadequate, as in most literature, but the keys which apply to males only are adequate. Chevreux and Fage (1925) give seven species and their keys are modified after Stebbing (1906). Barnard (1958) gives a catalogue of species, and other useful taxonomic works are those of Haswell (1882) describing 1 sp. from Australia, Sars (1894) 2 spp. from Norway, Stephenson (1929a) 2 spp. North Sea and Baltic, Shoemaker (1938) 1 sp. Mexico, Schellenberg (1942) 2 spp. Germany, Gurjanova (1951) 3 spp. U.S.S.R. and Myers (1968b) 3 spp. Central America.

Key to the Male ***MICRODEUTOPUS*** of the World

N.B. in most figures of limbs, article 1 is omitted so article 2 is the most proximal shown.

1 a. Gnathopod 2 chelate 2

b. Gnathopod 2 not chelate 3

2 a. Gnathopod 2 with articles 5 and 6 subequal in length and breadth, article 2 expanded, crenulated on anterior margin (Text-fig. 18d) . ***M. armatus*** (p. 129)

b. Gnathopod 2 with article 6 much shorter and broader than article 5, article 2 unexpanded, anterior margin smooth, (Text-fig. 19c) . . ***M. chelifer*** (p. 132)

3 a. Gnathopod 1 with the anterior margin of article 5 produced into a single tooth. Accessory tooth if present, arising within the posterior margin (Text-fig. 8b) . 4

b. Gnathopod 1 with article 5's anterior margin produced into 2 or more teeth (Text-fig. 2a) 7

4 a. Gnathopod 2 densely setose, the setae finely pectinate; article 4 extending over greater length of article 5 (Text-fig. 3i) . . . ***M. versiculatus*** (p. 101)

b. Gnathopod 2 moderately setose, the setae not pectinate; article 4 relatively short (Text-fig. 9c) . . . . (" ***anomalus*** " group) 5

5 a. Gnathopod 2 with articles 5 and 6 short and broad, palmar angle of article 6 almost transverse (Text-fig. 9a); uropod 3 with rami relatively short and broad ***M. damnoniensis*** (p. 114)

b. Gnathopod 2 with articles 5 and 6 slender, elongate, palmar angle of article 6 oblique (Text-fig. 9c); uropod 3 with rami relatively elongate and slender (Text-fig. 9e) 6

6 a. Gnathopod 1 with the anterior distal margin of article 5 produced into a slender, straight or inwardly curved tooth, generally with an accessory tooth arising near its base within the posterior margin (Text-fig. 8b) . ***M. anomalus*** (p. 110)

b. Gnathopod 1 with article 5's anterior margin produced into a broad based stout tooth, never with accessory tooth (Text-fig. 8h) . . . ***M. algicola*** (p. 117)

7 a. Gnathopod 1 with article 5 having the proximal (outer) of two teeth longer than the other (Text-figs. 2e, 22a) 8

b. Gnathopod 1's article 5 not as above 9

8 a. Antenna stout, subpediform, with the first flagellar article grossly developed (Text-fig. 4b); gnathopod 2 with article 2 elongate and slender (Text-fig. 3h) ***M. haswelli*** (p. 107)

b. Antenna relatively slender, the first flagellar article not as above (Text-fig. 21), gnathopod 2 with article 2 broad and short (Text-fig. 22g) . ***M. sporadhi*** (p.136).

9 a. Gnathopod 1 with the distal tooth on article 5 the longest (Text-fig. 2b) . . 10

b. Gnathopod 1 with the central tooth on article 5 the longest (Text-fig. 2d) . . ***M. stationis*** (p. 104)

10 a. Gnathopod 2 with article 2 convex anteriorly, crenated on the anterior margin (Text-fig. 3g) . . . . ***M. gryllotalpa*** (p. 98)

b. Gnathopod 2 with article 2 concave anteriorly and its anterior margin smooth (Text-fig. 14l) . . . . (" ***schmitti*** " ***group***) 11

11 a. Gnathopod 1 having article 5 with a tooth on the anterior margin (Text-fig. 13a) 12

b. Gnathopod 1 having article 5 without a tooth on the anterior margin (Text-fig. 13b) ***M. schmitti*** (p. 120)

12 a. Gnathopod 1 having article 6 with the palmar margin produced into a forward directed tooth opposable to article 7; posterior margins of articles 4, 5 and 6 with very long setae (Text-fig. 13e) . . . . . ***M. trichopus*** (p. 124)

b. Gnathopod 1 having article 6 with the palmar margin at most produced into a small lobe, which is never directed forward; posterior margin of article 4 only having very long setae, those of articles 5 and 6 being relatively short (Text-fig. 13a) . . . . ***M. hancocki*** (p. 124)

Microdeutopus gryllotalpa Costa

(Text-figs. 1a, 2a–c, 3a–c, g, m, 5b, 6c–d, 20a)

Microdeutopus gryllotalpa Costa, 1853 : 178; Costa, 1857 : 231, pl. 4, fig. 10; Boeck, 1870 : 156; Boeck, 1876 : 565, pl. 29, fig. 6; Blanc, 1884 : 75, pl. 4, figs. 82–90; Hoek, 1889 : 226; Della Valle 1893 : 411, pl. 1, fig. 12, pl. 11, figs. 25–43; Sars 1894 : 543, pl. 192, fig. 2; Sowinsky 1895 : 237, pl. 4, fig. 6; Sowinsky, 1898 : 480; Stebbing, 1906 : 590; Norman, 1907 : 368, pl. 16, fig. 3, pl. 17, figs. 6–7; Chevreux & Fage, 1925 : 299, fig. 310; Stephenson, 1927: 124; Stephensen, 1929a : 151, fig. 273; Oldevig, 1933 : 213, fig. 95; Cecchini & Parenzan, 1934 : 213, fig. 43; Loven, 1934: 6–8, fig. 2; Miloslavskaia, 1939a : 121; Schellenberg, 1942 : 186, fig. 154; Soika, 1949 : 199; Gurjanova, 1951 : 831, fig. 580; Barnard, 1958 : 29.
[*Non*] *Microdeutopus gryllotalpa* Bate, 1862 : 163, pl. 30, fig. 1.
[*Non*] *Microdeutopus gryllotalpa* Nebeski, 1880 : 45, fig. 41.
[*Non*] *Microdeutopus grillotalpa* [*sic*] Sowinsky, 1880 : 125, pl. 5, fig. 17 a–d.
Autonoe grandimana Bruzelius, 1859 : 26, pl. 1, fig. 5.
Microdeutopus grandimanus (Bruzelius) Bate, 1862 : 378.
Microdeutopus minax Smith, 1874 : 562.
Microdeutopus bidens Sowinsky, 1880 : 129, pl. 5, fig. 18.
[?]*Amphithoe salenskii* Carus, 1885 : 396.
Microdeuteropus gryllotalpa (Costa) Norman, 1886 : 16; Chevreux & Bouvier, 1893 : 133.
Microdeuteropus minax (Smith) Norman, 1886 : 17.

TYPE LOCALITY. Lago di Fusaro, Italy.

DIAGNOSIS OF MALE. *Antennule* about half the body length, the first peduncular article slightly shorter than the second, the third about one third the length of the second; flagellum longer than the peduncle normally with up to twenty-two articles (maximum recorded twenty-six); accessory flagellum with two articles, the second article rudimentary. *Antenna* slightly under two thirds the length of the antennule, the fourth and fifth peduncular articles subequal; flagellum shorter than the fifth peduncular article, normally with up to nine articles (maximum recorded eleven). *Peraeon* segments 2–7 each with a process in the mid-ventral line, those of segments 2 and 3 short, straight, those of segments 4–7 short, robust, posteriorly directed; processes 6 and 7 with short setae arising from their posterior margins. *Gnathopod* 1 with article 1 moderately produced anteriorly, acute; article 2 short and expanded distally; article 5 immensely expanded, in some specimens as broad as long, the posterior distal margin produced into two to four teeth, of which the most distal is always the longest; article 6 short, the posterior margin irregularly lobed; article 7 sometimes short and robust, sometimes relatively long and slender. *Gnathopod* 2 with article 2 greatly expanded, the anterior margin convex and crenated; articles 5 and 6 subequal in length, 5 slightly the broader, articles 4, 5 and 6 with long pectinate setae on the anterior margins. *Uropod* 3 with rami equal in length to the peduncle exopodite slightly the longer of the two rami; each ramus with a transverse row of three closely associated spines on the outer dorsal margin, together with a number of paired and solitary spines of variable distribution, terminal setae relatively long. *Telson* with each terminal crest bearing on its distal dorsal margin, a group of up to six setae.

Maximum size of male: 8 mm.

Female. As the male except for the absence of ventral peraeon processes and the structure of the sexually dimorphic gnathopoda.

Gnathopod 1 with article 2 moderately expanded; articles 5 and 6 subequal in length, 5 slightly the broader, 6 with the anterior and posterior margins roughly parallel; article 7 equal in length to the angular palmar region. *Gnathopod* 2 with

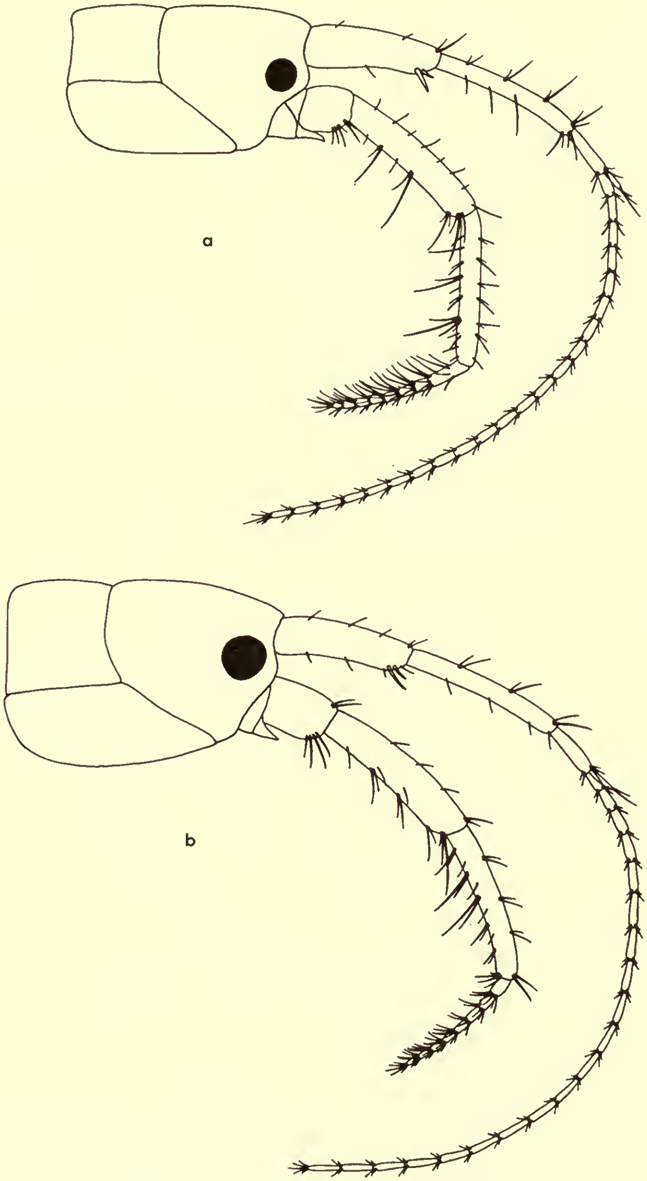

Fig. 1. *Microdeutopus gryllotalpa* Costa. (a) Male head, Swansea, Wales. *Microdeutopus versiculatus* (Bate). (b) Male head, Falmouth Harbour, England.

article 2 slightly expanded, crenulated on the anterior margin; articles 5 and 6 elongate, subequal; articles 4, 5 and 6 with pectinate setae on their anterior margins.

Maximum size of female: 10 mm.

Discussion. *M. gryllotalpa* is closely related to *M. versiculatus* but differs in both sexes by the second gnathopod (Text-figs. 3g, 5b) not having the fourth article greatly produced along the posterior border of the fifth, nor the fifth and sixth

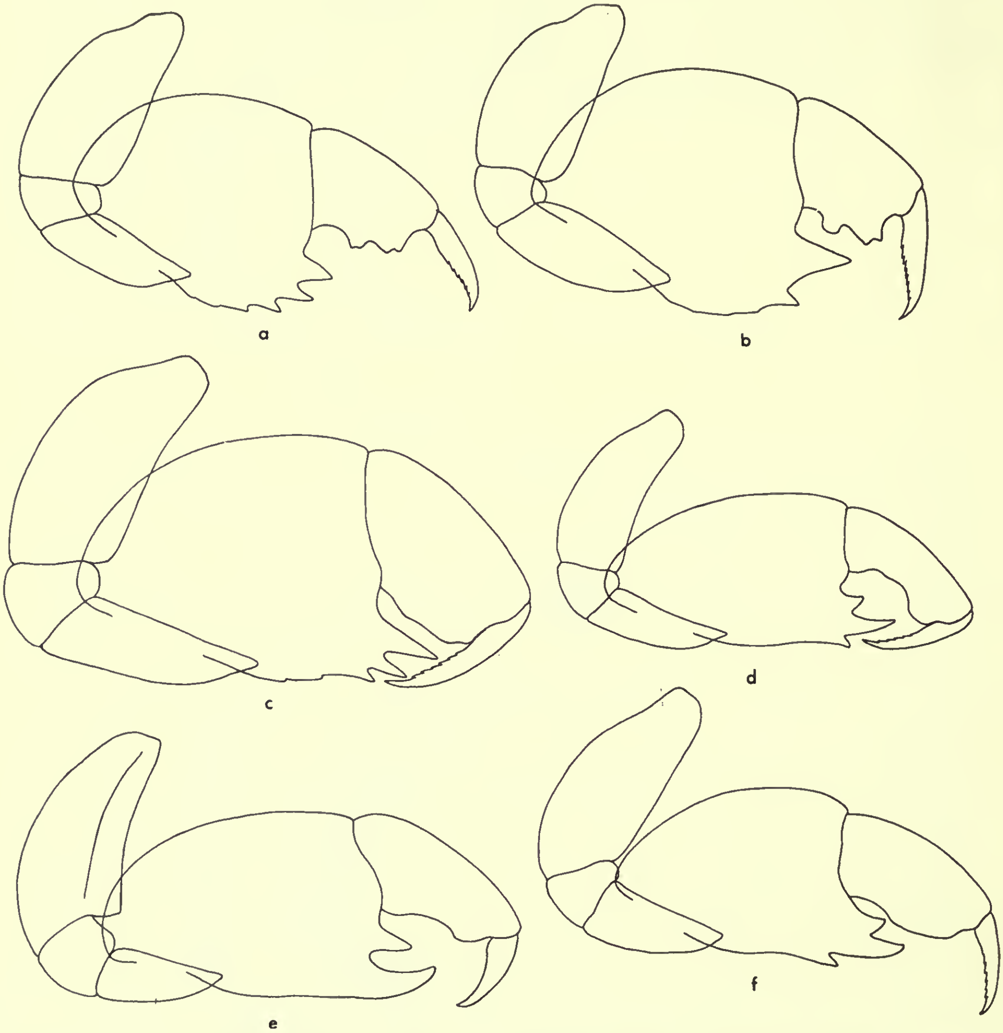

Fig. 2. *Microdeutopus gryllotalpa* Costa. (a) Male gnathopod 1, Swansea, Wales. (b) Male gnathopod 1, Swansea, Wales. (c) Male gnathopod 1, Isefjord, Denmark. *Microdeutopus stationis* Della Valle. (d) Male gnathopod 1, St. Peter's Port, Guernsey. (f) Male gnathopod 1, Naples, Italy. *Microdeutopus haswelli* Stebbing. (e) Male gnathopod 1, Port Jackson, Australia (Holotype).

articles so markedly elongate and slender. Females of *M. gryllotalpa* are readily identifiable by the structure of the fifth article of the second gnathopod (Text-fig. 5b), which has long pectinate setae arising from the entire length of the anterior margin, whereas in all other *Microdeutopus* species (except *M. versiculatus*) the long setae arise from the anterior corner only of the fifth article.

ECOLOGY. In the intertidal zone in rock pools amongst *Chaetomorpha* and other algae; amongst *Zostera* spp.; and in salt marshes (Chevreux & Fage, 1925), often associated with *Ruppia maritima* as at Roscoff (Truchot, 1963). Also occurring sub-littorally to a depth of about 150 metres on oyster beds, and amongst algae, tunicates, sponges, polyzoans, *Mytilus* etc., always in areas of high detritus accumulation. It particularly favours docks and other man-made installations, and is frequently associated with *Corophium acherusicum* Costa in both the Palearctic and Nearctic regions.

DISTRIBUTION. From the Lofoten Islands southwards along the coasts of Norway, Sweden, Denmark, including the Baltic, and Holland, around the coasts of the British Isles, chiefly in the south-west, along the Atlantic coasts of France, Spain and Portugal, and in the Mediterranean Ligurian, Tyrrhenean, Adriatic, Aegean and Black Seas. Also, on the north-eastern seaboard of the United States of America (Massachusetts, Rhode Island and Connecticut).

Microdeutopus versiculatus (Bate)

(Text-figs. 1b, 3i, k, 5a, 6a–b, 20c)

Lembos versiculatus Bate, 1856 : 58; Bate, 1857 : 142.
Microdeutopus versiculatus Bate, 1862 : 165, pl. 30, fig. 5; Bate & Westwood 1863 : 295; Walker, 1895 : 469; Chevreux 1900 : 89; Stebbing, 1906 : 593.
Microdeuteropus versiculatus (Bate) Norman, 1869a : 282; Stebbing, 1874 : 12, pl. 1, figs. 2, 2a–f. Chevreux & Bouvier, 1893 : 134.
Autonoe longipes (Lilljeborg) Boeck, 1876 (pro-parte) : 574.
Autonoe versiculata (Bate) Norman, 1886 : 17.
Microdeutopus anomalus (Rathke) Della Valle, 1893 (pro-parte) : 418.
Coremapus versiculatus (Bate) Norman, 1905b : 78; Chevreux & Fage, 1925 : 301, fig. 312; Stephensen, 1929a : 152, fig. 276; Cecchini & Parenzan, 1934 : 217, fig. 45; Miloslavskaia, 1939a : 125, fig. 25; Soika, 1949 : 200; Gurjanova, 1951 : 835, fig. 585; Barnard, 1958 : 29.

TYPE LOCALITY. Plymouth, Devon, England.

DIAGNOSIS OF MALE. *Antennule* about equal to the body length, the first peduncular article slightly shorter than the second, the third about one third the length of the second; flagellum almost twice the length of the peduncle, normally with up to twenty articles (maximum recorded twenty-two); accessory flagellum with two articles, the second article rudimentary. *Antenna* little more than half the length of the antennule, the fourth peduncular article slightly longer than the fifth; flagellum shorter than the fifth peduncular article, normally with up to eight articles (maximum recorded nine). *Peraeon* segments 2–7 each with a process in the mid-ventral line; that of segment 2 slender, spiniform, directed anteriorly; those of segments 3 and 4 slender, spiniform, straight; those of 5–7 robust, decreasing in size antero-posteriorly, with processes 6 and 7 having setae arising from their posterior margins. *Gnathopod* 1 with article 1 moderately produced anteriorly, acute; article 2 considerably expanded; article 5 much enlarged, longer than broad, the posterior distal angle produced into a single, robust tooth; article 6 short, the posterior margin irregularly lobed; article 7 short and robust. *Gnathopod* 2 with article 2 somewhat expanded; article 4 well developed, extending over the greater length of the posterior margin of article 5; article 5 longer than article 6, elongate and slender, about three times as long as broad; article 6 also very long and slender, about three and a half times as long as broad; article 7 very short, long pectinate setae arising from the anterior margins of articles 4, 5 and 6. *Uropod* 3 with rami sub-equal, equal in length to the peduncle; exopodite with a transverse row of three closely associated spines on the outer-dorsal margin, basal to which is a solitary spine; endopodite with a similar transverse row of closely associated spines on the outer-dorsal margin, and in addition on the inner margin, a series of well separated spines; terminal setae of both rami relatively long. *Telson* with each terminal crest bearing on its distal dorsal margin a group of two to three setae.

Maximum size of male: 7 mm.

FEMALE. As the male except for the structure of the sexually dimorphic gnathopoda and absence of ventral peraeon processes. *Gnathopod* 1 with article 2 short and considerably expanded, about two thirds as broad as long; article 5 scarcely longer than article 6, with a dense clothing of comb setae along the entire length of the posterior border; article 6 almost as broad as 5, with the anterior and posterior margins roughly parallel; article 7 moderately long, equal in length to the palmar region. *Gnathopod* 2 with article 2 elongated and slender, otherwise identical with the corresponding appendage of the male.

Maximum size of female: 8 mm.

DISCUSSION. First designated as a *nomen nudum* by Bate (1856) the species was later described from the female (Bate, 1857, 1862). The male was first described by Norman (1868) and later by Stebbing (1874) who also gave figures. The suggestion that a monotypic genus should be erected for this species (Norman, 1905b) is not accepted. The present species bears a close relationship with *M. gryllotalpa* Costa in the similarity of the male first gnathopod of the two species. That of *M. versiculatus* (Text-fig. 3k) differs in having a single tooth on the posterior distal angle of article 5, whereas in *M. gryllotalpa* (Text-figs. 2a–c) there are two to four. The two species are also similar in the structure of the male second gnathopod. Article 2 of that appendage is expanded, though less markedly in *M. versiculatus* (Text-fig. 3i) than in *M. gryllotalpa* (Text-fig. 3g) and article 5 has pectinate setae arising from the entire anterior margin (also a character of the female). Finally, males of both species have ventral processes on all peraeon segments except the first. The remarkable slender, setose second gnathopod of *M. versiculatus* (Text-fig. 5a), which led Normon (1905b) to erect a monotypic genus for the species, is an extreme modification of the type found in *M. gryllotalpa* and serves to distinguish *M. versiculatus* in both sexes from all other *Microdeutopus* species.

ECOLOGY. In the intertidal zone (Oldany, Sutherland), but much more frequently in the sub-littoral to a depth of about 150 metres (off the Shetland Islands) amongst

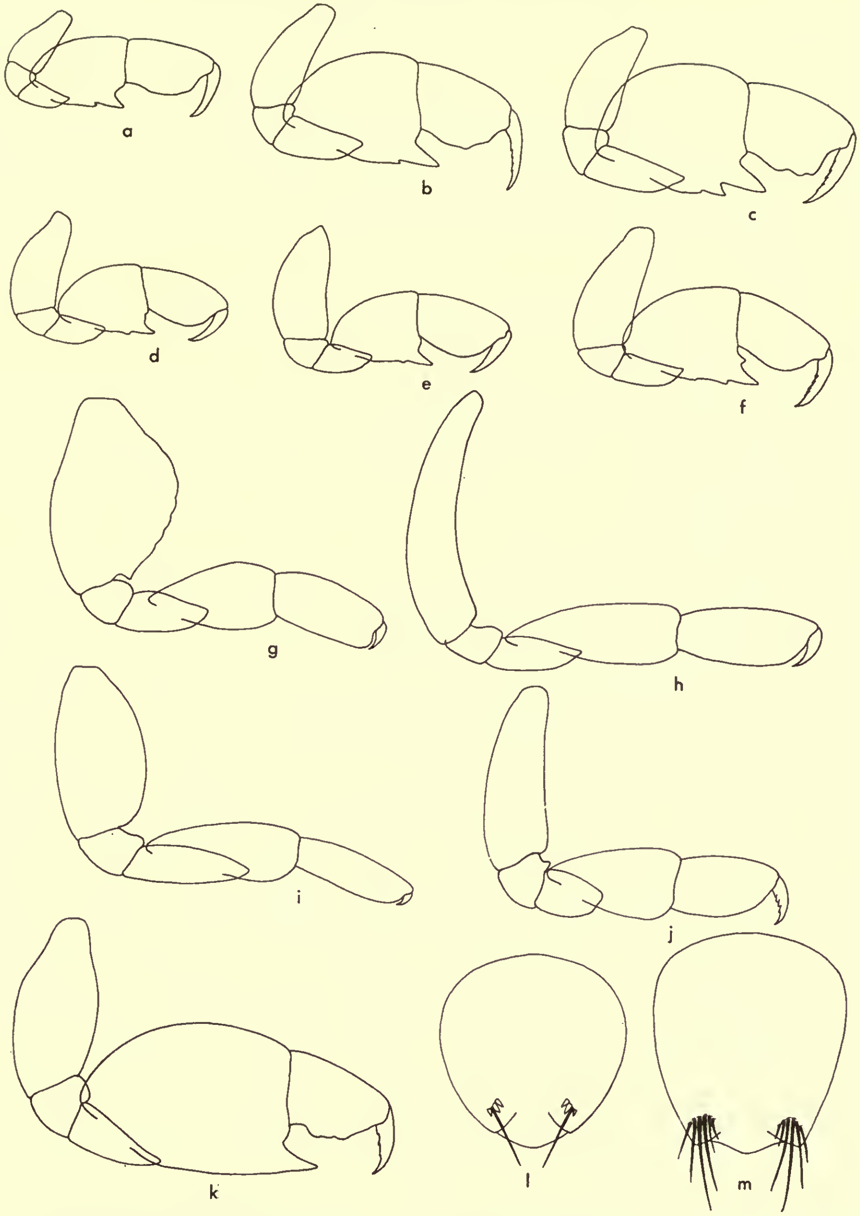

Fig. 3. *Microdeutopus gryllotalpa* Costa. (a) Male gnathopod 1, 1·8 mm. ♂, Swansea, Wales. (b) Male gnathopod 1, 2·9 mm. ♂, Swansea, Wales. (c) Male gnathopod 1, 3·9 mm. ♂, Swansea, Wales. (g) Male gnathopod 2, Swansea, Wales. (m) Male telson, Swansea, Wales. *Microdeutopus stationis* Della Valle. (d) Male gnathopod 1, 1·9 mm. ♂, Naples, Italy. (e) Male gnathopod 1, 2·0 mm. ♂, Naples, Italy. (f) Male gnathopod 1, 3·5 mm. ♂, Naples Italy. (j) Male gnathopod 2, Naples, Italy. (l) Male telson, Naples, Italy. *Microdeutopus haswelli* Stebbing. (h) Male gnathopod 2, Port Jackson, Australia (Holotype). *Microdeutopus versiculatus* (Bate). (i) Male gnathopod 2, Plymouth, Devon. (k) Male gnathopod 1, Plymouth, Devon.

algae, especially cystoseires and corallines, polyzoans, *Mytilus* etc. in areas of high detritus accumulation.

DISTRIBUTION. Along the south and west coasts of the British Isles to the Shetlands, in the Channel Islands and the adjoining French coast, Bay of Biscay (Houat, Arcachon), the Atlantic coasts of Spain and Portugal, Senegal and the Azores. Also around the coasts of the Mediterranean, Tyrrhenian and Adriatic seas, and in the Black sea (north-east of Cape Caliacra, Roumania).

Microdeutopus stationis Della Valle

(Text-figs. 2d, f, 3d–f, j, l, 4a, 5c, 6e–f, 20e)

Microdeutopus gryllotalpa Nebeski, 1880 : 45, fig. 41.

Microdeutopus stationis Della Valle, 1893 : 415, pl. 5, fig. 2, pl. 10, figs. 31–41; Stebbing, 1906 : 590; Norman, 1907 : 368, pl. 16, fig. 4, pl. 17, figs. 8–11; Chevreux & Fage, 1925 : 300, fig. 311; Cecchini & Parenzan, 1934 : 216, fig. 44; Miloslavskaia, 1939a : 122; Gurjanova, 1951 : 832, fig. 581; Barnard, 1958 : 29.

[*Non*] *Microdeutopus stationis* Sowinsky, 1895 : 237, pl. 4, figs. 1–5; Sowinsky, 1898 : 480.

TYPE OF LOCALITY. Naples, Italy.

DIAGNOSIS OF MALE. *Antennule* about equal to the body length, the first peduncular article slightly shorter than the second, the third less than one third the length of the second; flagellum twice the length of the peduncle, normally with up to twenty-six articles (maximum recorded twenty-nine); accessory flagellum with two to five articles, the terminal article rudimentary. *Antenna* two thirds the length of the antennule, the fourth and fifth peduncular articles subequal; flagellum equal in length to the fifth peduncular article, normally with up to twelve articles (maximum recorded fourteen). *Peraeon* segments 2–4 each with a process in the mid-ventral line, that of segment 2 slender spiniform, straight, those of segments 3 and 4 becoming progressively shorter and more robust. *Gnathopod* 1 with article 1 strongly produced anteriorly, very attenuated; article 2 scarcely expanded; article 5 very enlarged, longer than broad, the posterior distal angle produced into three teeth of which the central is the longest, the inner two slightly recurved; article 6 short, the posterior margin convex distally, concave basally; article 7 long and slender. *Gnathopod* 2 with article 2 not expanded; article 5 longer and slightly broader distally than article 6. *Uropod* 3 with the rami slightly shorter than the peduncle, the expodite slightly the longer of the two rami, bearing on its outer distal margin a group of three closely associated elongate spines, with a pair of spines (of which one is elongate) basal to these and not infrequently a further solitary spine basal to the pair; inner margin of exopodite with one or two solitary spines; endopodite outer margin with a pair of spines, basal to which is a solitary spine; inner margin with up to two pairs of spines and a solitary spine; terminal spines and setae of both rami very short. *Telson* with each terminal crest bearing on its distal dorsal margin, a group of three short stout spines and a single fine seta.

Maximum size of male: 10 mm.

FEMALE. As the male, except for the structure of the sexually dimorphic gnathopoda, and absence of ventral peraeon processes. *Gnathopod* 1 with article 2 scarcely

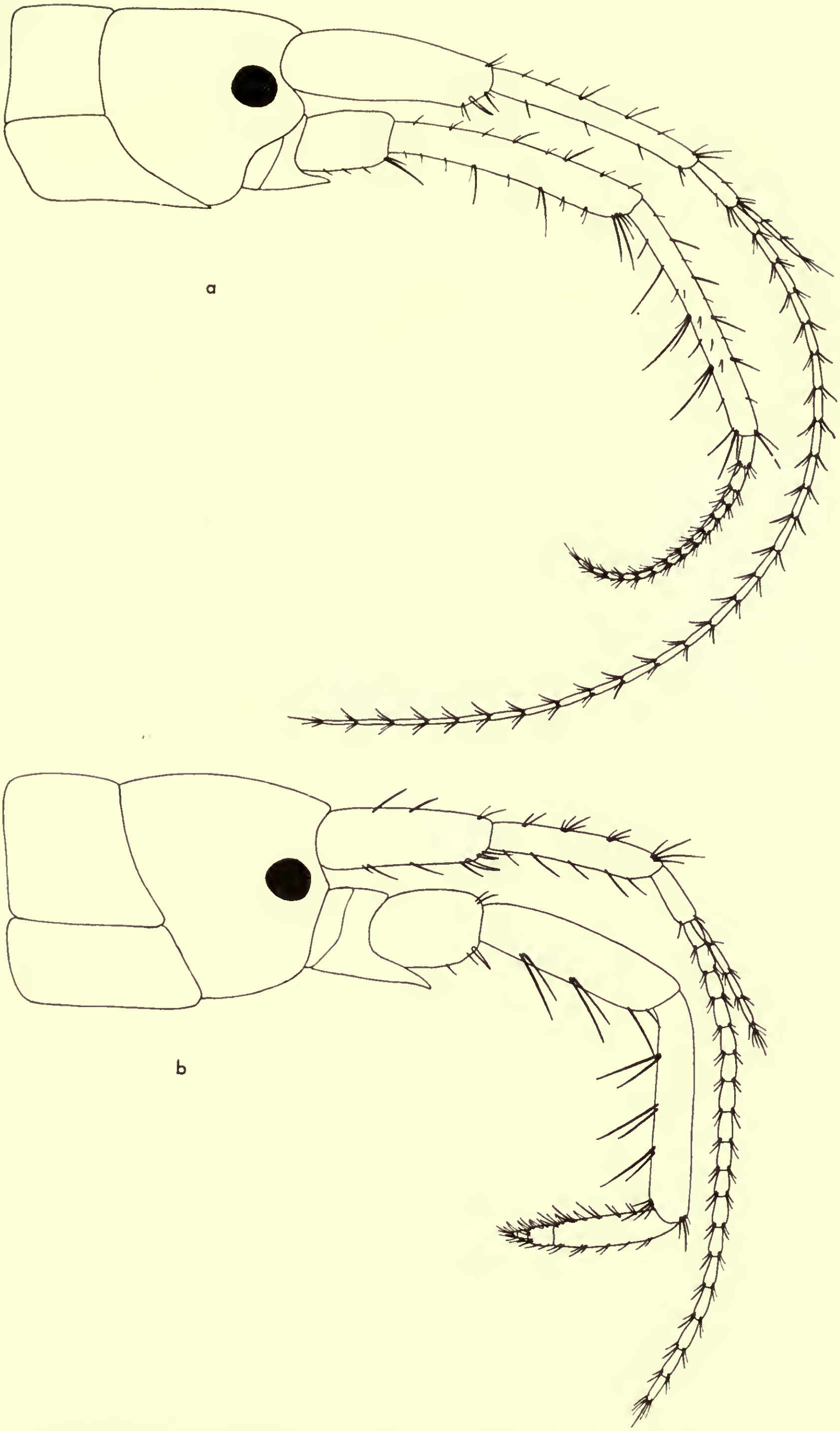

FIG. 4. *Microdeutopus stationis* Della Valle. (a) Male head, St. Peter's Port, Guernsey. *Microdeutopus haswelli* Stebbing. (b) Male head, Port Jackson, Australia (Holotype).

expanded, articles 5 and 6 subequal in length, the sixth distinctly broader distally, narrowing at the junction with the fifth article, the palmar angle smoothly rounded; article 7 elongate and slender. *Gnathopod* 2 with article 2 relatively slender, article 5 slightly shorter than article 6, setae not pectinate.

Maximum size of female : 12 mm.

DISCUSSION. The species was first described by Nebeski (1880) from the Adriatic, and erroneously ascribed to *M. gryllotalpa* Costa. That author's illustrations (Nebeski, 1880, fig. 41) of the growth stages of the male gnathopod 1 clearly indicate that he was dealing with the species later described by Della Valle under the name *M. stationis*.

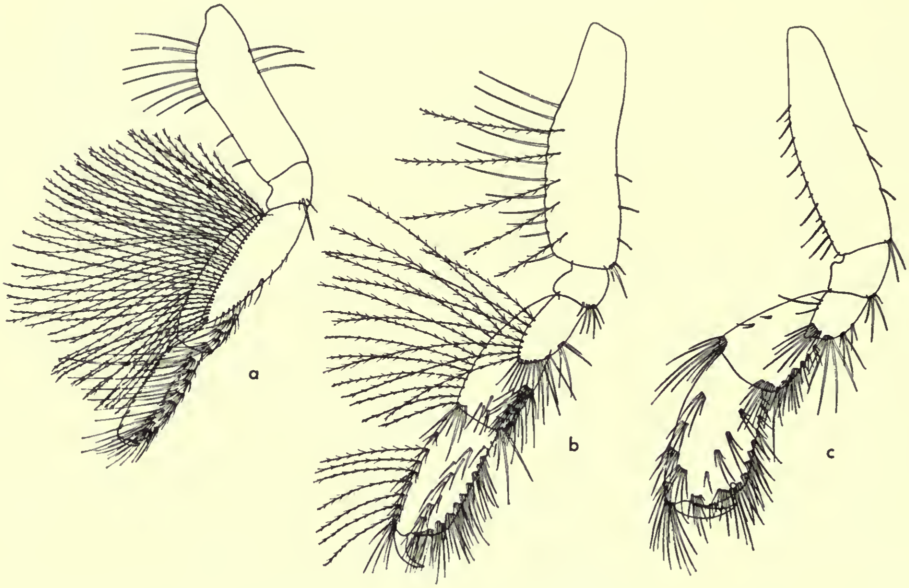

FIG. 5. *Microdeutopus versiculatus* (Bate). (a) Female gnathopod 2, Plymouth, Devon. *Microdeutopus gryllotalpa* Costa. (b) Female gnathopod 2, Swansea, Wales. *Microdeutopos stationis* Della Valle. (c) Female gnathopod 2, Naples, Italy.

M. stationis is easily distinguishable in the male from all other described species in the genus by having the posterior distal angle of article 5 of the first gnathopod (Text-figs. 2d, f) produced into three teeth, of which the central is the longest. Females have few diagnostic characters, but important characters taken in combination are the telson (Text-fig. 31) bearing both spines and setae, uropod 3 (Text-fig. 6f) with groups of spines on the rami, accessory flagellum with two to four articles and long slender antenna with multi-articulate flagellum.

ECOLOGY. Recorded in *Sacchoriza* holdfasts, among *Posidonia*, on oyster beds and over fine sands, in regions of relatively low detritus contamination, in the sublittoral to a depth of 50 metres.

DISTRIBUTION. Guernsey (St. Peter's Port), France (Arcachon, Roscoff, Perros Guirec), Corsica (Ajaccio, Bonifacio), Algeria (Bône, La Calle), Tunisia (Golfe de Gabes), Italy (Naples, Trieste), Greece (Khios).

Microdeutopus haswelli Stebbing

(Text-figs. 2e, 3h, 4b)

Microdeuteropus chelifer Hasell, 1879 : 340, pl. 22, fig. 3; Della Valle, 1893 : 421.
Microdeutopus chelifer Haswell, 1882 : 265.
Microdeutopus haswelli Stebbing, 1899 : 350; Stebbing, 1906 : 591; Stebbing, 1910 : 647; Sheard, 1937 : 26; Barnard, 1958 : 29.

TYPE LOCALITY. Clark Island, Port Jackson, Australia.

The present species is represented by a single male specimen in Haswell's collections, at the Australian Museum, Sydney. Haswell did not designate types for any of his material, but this specimen is almost certainly the holotype, agreeing in the main with Haswell's description, and is here considered as such. An expanded description of the more relevant features of the holotype is given. The range of variation of this species is not known, as further material has not been forthcoming.

DESCRIPTION OF MALE HOLOTYPE. Head lateral lobes slightly produced, obtuse; eyes round. *Antennule* slightly less than half the body length, the first and second peduncular articles subequal, the third slightly over a third the length of the second; flagellum longer than the peduncle, with seventeen articles; accessory flagellum with five articles, the fifth article rudimentary. *Antenna* shorter than the antennule, sub-pediform, the fifth peduncular article slightly longer than the fourth; flagellum with four articles, the first article long and robust, over half the length of the fifth peduncular article, the second short, the third and fourth articles progressively shorter, obscurely articulate. *Gnathopod* 1 with article 1 moderately produced anteriorly, obtuse; article 2 short and expanded, the anterior margin excavate; article 5 much enlarged, longer than broad, the posterior distal angle produced into two teeth, of which the outer is the longer and recurved; article 6 short, the posterior margin concave centrally; article 7 very stout. *Gnathopod* 2 with article 2 very elongated and slender, concave anteriorly, articles 5 and 6 slender with article 5 slightly the longer. *Epimeral plate* 3 with the posterior free corner produced into a tooth, above which is inserted a short seta. *Uropod* 3 with the peduncle exceeding the length of the very short and stout rami, of which the exopodite is very slightly the longer; each ramus with a terminal group of setae which exceed the length of the ramus. *Telson* with the terminal crests moderately well developed, each bearing on its distal, dorsal margin, a group of three setae, of which the central is the longest.

Length : 4·5 mm.

DISCUSSION. The very robust, sub-pediform antenna, (Text-fig. 4b) with the flagellum very reduced and the first flagellar article robust, approaches the condition found in many Corophiidae. However, the lateral compression of the urosome, biramous third uropoda, and moderately well developed coxae, are characteristic of aorid/photid stock. *M. haswelli* differs from all other *Microdeutopus* species, except *M. sporadhi* sp. nov. (p. 136), in having the posterior distal angle of article 5 of the male first gnathopod (Text-fig. 2e) produced into two teeth, of which the outer is the longer. The elongated, slender article 2 of the male second gnathopod (Text-fig. 3h) is also a distinctive feature.

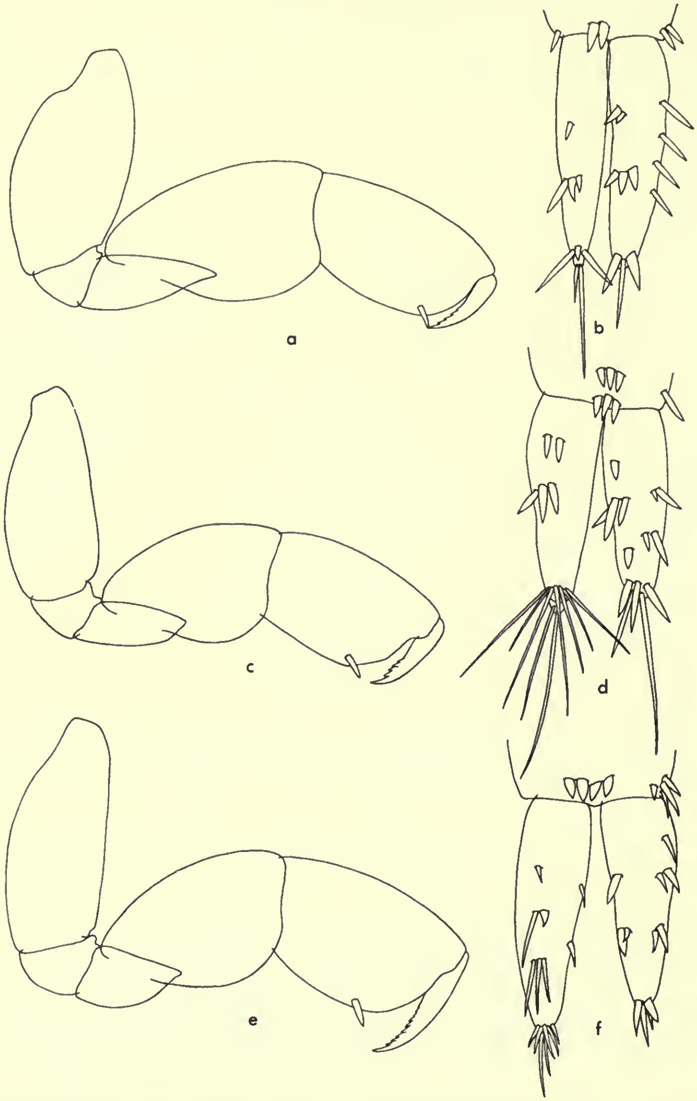

Fig. 6. *Microdeutopus versiculatus* (Bate). (a) Female gnathopod 1, Plymouth, Devon. (b) Male uropod 3, Falmouth, Cornwall. *Microdeutopus gryllotalpa* Costa. (c) Female gnathopod 1, Swansea, Wales. (d) Male uropod 3, Arcachon, France. *Microdeutopus stationis* Della Valle. (e) Female gnathopod 1, Naples, Italy. (f) Male uropod 3, Naples, Italy.

ECOLOGY. Unknown.

DISTRIBUTION. Not yet recorded from other than the type locality.

THE " ANOMALUS " GROUP OF SPECIES

The systematics of the anomalus group of species has long been under dispute. In 1856 Bate erected two species, *Lembos damnoniensis* and *L. cambriensis*, but gave no descriptions and only in the following year attributed to the former species " first hand with a thumb on carpus " to the latter " first hand without thumb ". White (1857), no doubt in error, transposed the " mn " in *L. damnoniensis*, to " nm " in *L. danmoniensis*, and later Bate (1862) and Bate and Westwood (1863) relegated *L. cambriensis* to a synonym of *M. anomalus* (Rathke) and *L. damnoniensis* to a synonym of *M. gryllotalpa* Costa. Norman (1868) considered that *M. gryllotalpa* Bate represented a young male *M. anomalus*, but later (Norman 1905b) decided that *M. damnoniensis* Bate, was a distinct species, and that *M. gryllotalpa* Bate (non *M. gryllotalpa* Costa) represented that species. Sars (1894) figures a species under the name *M. propinquus* Sars, but in the text relegates it to a synonym of *M. danmoniensis* (Bate) (altered presumably in error, or following White, 1857, from *M. damnoniensis*). Stebbing (1906) considered that *M. propinquus* Sars was not synonymous with *M. damnoniensis* (Bate) and reinstated it as a distinct species with synonym *M. danmoniensis* Sars (non *M. damnoniensis* (Bate)). Andersson (1954) considered *M. propinquus* Sars to be a juvenile form of *M. anomalus* (Rathke) and in the synonymy also listed *L. damnoniensis* Bate. Della Valle (1893) described a new species *M. algicola*, and placed *M. damnoniensis* in the synonymy of *M. anomalus* (Rathke).

Present investigations suggest that there are three distinct species in the " *anomalus* " group; *M. anomalus* (Rathke), *M. damnoniensis* (Bate) and *M. algicola* Della Valle.

Males of the " *anomalus* " group of species are distinguished from those of all other *Microdeutopus* species, except *M. versiculatus* (Bate) *M. chelifer* (Bate) and *M. armatus* Chevreux by having the posterior margin of gnathopod 1 produced into a single marginal tooth. In *M. anomalus* an accessory tooth is usually present, but this always arises *within* the posterior margin. They differ from the above three species in the structure of gnathopod 2, which is neither chelate as in *M. chelifer* and *M. armatus* not densely setose as in *M. versiculatus*. Females of the " *anomalus* " group of species are notable for their lack of diagnostic features, and are therefore identifiable only by negative characters. They are distinguishable from *M. versiculatus*, *M. gryllotalpa* and *M. stationis* by the absence of paired spines from the rami of the third uropod, from the first two species by the absence of pectinate setae on gnathopod 2. They differ also from *M. stationis* and from the " *schmitti* " group of species by the lack of any spines as distinct from setae on the telson terminal crests, and from *M. armatus* by the lack of any pronounced projection at the anterodistal corner of article 2 or gnathopod 2. Within the " *anomalus* " group of species the identification of females is even more difficult, particularly in the absence of males. In practice, when two or more of the " *anomalus* " group occur together in a sample, the females have been separated with some degree of accuracy and grouped together with the corresponding males, according to characters summarized in Table 1. Owing to confusion between the three species, records are unreliable and so the ecology and distribution of the "*anomalus*" group of species is poorly known.

Character	*M. anomalus*	*M. damnoniensis*	*M. algicola*
1. Maximum size	10 mm.	4·5 mm.	4·5 mm.
2. Antennule			
a. Ratio of peduncular articles	$1 : 1\frac{1}{3} : \frac{1}{2}$	$1 : 1 : \frac{1}{2}$	$1 : 1 : \frac{1}{3}$*
b. Average number of flagellar articles	23	14	20*
c. Number of articles to accessory flagellum excluding vestigial terminal article	3–4	1	2
3. Uropod 3			
a. Peduncle	Flanges poorly developed, dorsal and inner longest	Flanges well developed inner much the longest	as *damnoniensis*
b. rami	slender, elongate	broad, robust	as *anomalus*

TABLE 1. The main identification characters for females of the "anomalus" group of species. * = From Della Valle (1893).

Microdeutopus anomalus (Rathke)

(Text-figs. 7a, 8a–e, 9c, e, 10c, f, 20b, d)

Gammarus anomalus Rathke, 1843 : 63, pl. 4, fig. 7; Lilljeborg, 1855 : 457.
Autonoe anomala (Rathke) Bruzelius, 1859 : 25, fig. 4.
Autonoe sp. Smith, 1874 : 562.
Microdeutopus anomalus (Rathke) Boeck, 1870 : 157; Catta, 1875 : 167; Boeck, 1876 : 567, pl. 25, fig. 5; Della Valle, 1893 : 417, pl. 56, fig. 41; Sars, 1894 : 540, pl. 191; Sowinsky, 1898 : 480, pl. 10, figs. 20–24; Stebbing, 1906 : 591; Kunkel, 1910 : 76, fig. 29; Chevreux & Fage, 1925 : 298, fig. 309; Stephensen, 1927 : 124; Stephensen, 1929a : 152, fig. 275; Oldevig, 1933 : 212, fig. 94; Miloslavskaia, 1939a : 123; Carausu & Carausu, 1942 : 74, fig. 5; Schellenberg, 1942 : 188, fig. 155; Soika, 1949 : 198; Gurjanova, 1951 : 833, fig. 582; Andersson, 1954 : 252, figs. 1–4; Barnard, 1958 : 29.
[*Non*] *Microdeutopus anomalus* Bate, 1862 : 164, pl. 30, fig. 3.
Microdeuteropus anomalus (Rathke) Norman, 1869a : 281; Norman, 1886 : 16.
Microdeutopus propinquus Sars, 1894 : 542, pl. 192; Stebbing, 1906 : 592; Stephensen, 1927 : 125; Stephensen, 1929a : 152, fig. 274; Oedevig, 1933 : 212, fig. 95; Schellenberg, 1942 : 189, fig. 156; Dahl, 1946 : 5; Gurjanova, 1951 : 834, fig. 583.
Microdeutopus danmoniensis [*sic*] Sars, 1894 : 542, pl. 192.
Microdeutopus stationis Sowinsky, 1895 : 237, pl. 4, figs. 1–6.

TYPE LOCALITY. Christiansund, Norway.

Diagnosis of male. *Antennule* about two thirds the body length, the first peduncular article shorter than the second, the third about one third the length of the second; flagellum slightly less than twice the length of the peduncle, normally with up to twenty-three articles (maximum recorded twenty-seven); accessory flagellum with four to five articles, the terminal article of which is rudimentary. *Antenna* two thirds the length of the antennule, the fourth and fifth peduncular articles subequal; flagellum about equal to the fifth peduncular article, normally with up to six articles (maximum recorded eight). *Peraeon* segments 2–4 each with a spine in the mid-ventral line, those of segments 2 and 3 the longest and most slender, that of segment 4 the shortest and most robust; segment 5 in some specimens with a vestigial spine. *Gnathopod* 1 with article 1 strongly produced anteriorly, very attenuated; article 2 elongate and relatively slender; article 5 very enlarged, longer than broad, the posterior distal angle produced into a straight or slightly recurved tooth, at the base of which in mature specimens is characteristically an accessory tooth, which arises within the posterior margin and is not an extension of it as in other *Microdeutopus* species; article 6 with the posterior margin concave, excepting the palmar angle; article 7 variable, usually relatively long and slender. The accessory tooth on article 5 varies considerably in size, sometimes being so reduced that it does not project over the posterior margin and appears obsolete; occasionally in adults and frequently in juveniles it is absent. The aberrant form of this species described and figured by Chevreux and Fage (1925) with two accessory teeth, has not been observed in the present investigations. *Gnathopod* 2 with article 2 unexpanded; articles 5 and 6 elongate, 5 slightly the broader; article 6 almost three times as long as broad, with the palmar angle oblique; article 7 relatively long. *Uropod* 3 with the peduncle slender, its outer, inner and dorsal margins each produced into a flange of which the dorsal and inner are the most pronounced; rami equal to or slightly exceeding the length of the peduncle; endopodite slightly shorter than the exopodite, with four spines on the inner margin and two on the outer, none of which are closely associated; exopodite with two spines on the outer margin only. *Telson*, with each terminal crest bearing on its distal dorsal margin, a pair of unequal setae.

Maximum size of male : 8 mm.

Female, As the male, except for the structure of the sexually dimorphic gnathopoda, and absence of ventral peraeon spines. *Gnathopod* 1 with article 1 somewhat produced anteriorly, rounded; article 2 unexpanded; article 6 longer than article 5, distinctly broader distally, and constricted at the junction with article 5; article 7 longer than the palmar region. *Gnathopod* 2 with article 2 elongate and slender; article 6 considerably longer and more slender than article 5.

Maximum size of female : 10 mm.

Discussion. *M. anomalus* is distinguishable in the male, in its typical form, from all other *Microdeutopus* spp. by the presence of an accessory tooth, arising within the posterior margin of article 5 of gnathopod 1 (Text-figs. 8a, b, d, e). Past workers have described *M. anomalus* as having this accessory tooth (or teeth) always present, although this is by no means the case, particularly in immature material, and have frequently utilized this character as a basis for a key (Stebbing, 1906, Chevreux &

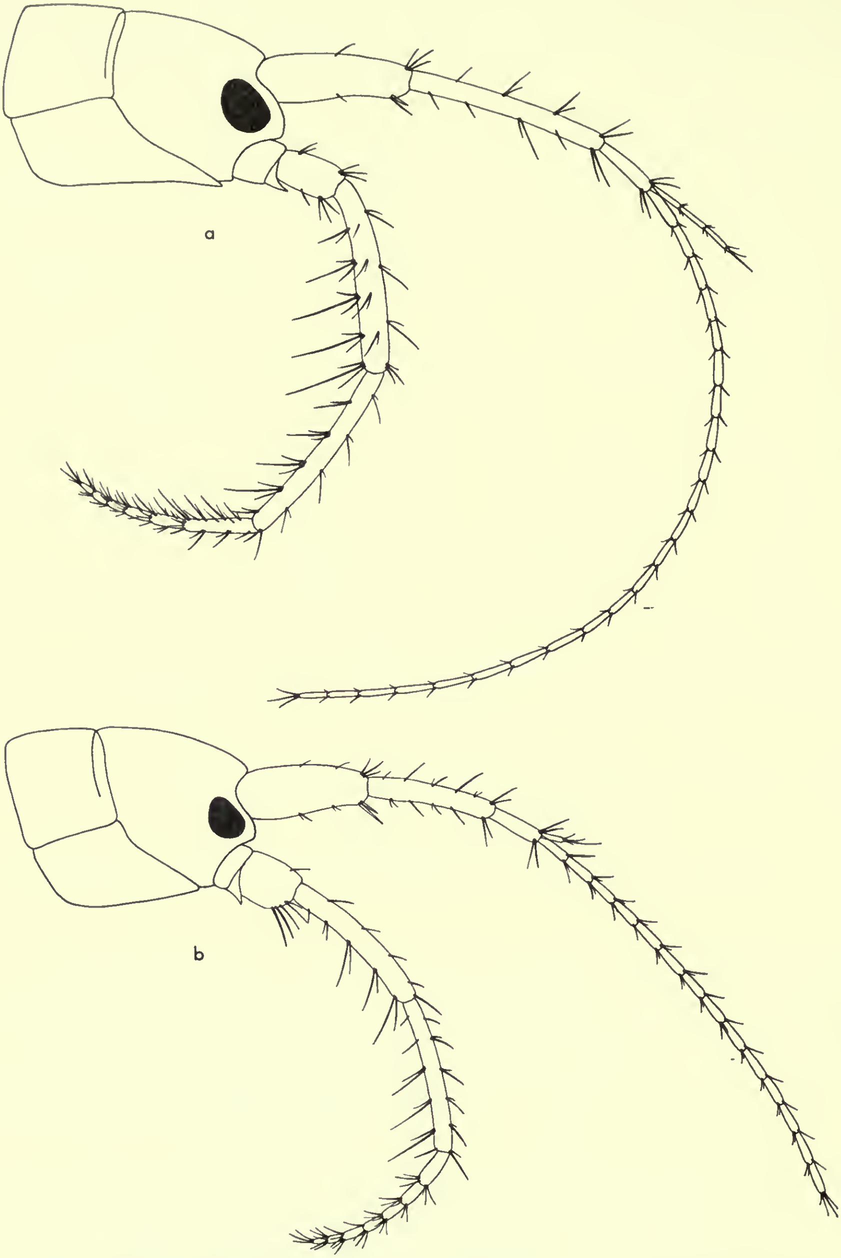

FIG. 7. *Microdeutopus anomalus* (Rathke). (a) Male head, Plymouth, Devon. *Microdeutopus damnoniensis* (Bate). (b) Male head, Plymouth, Devon.

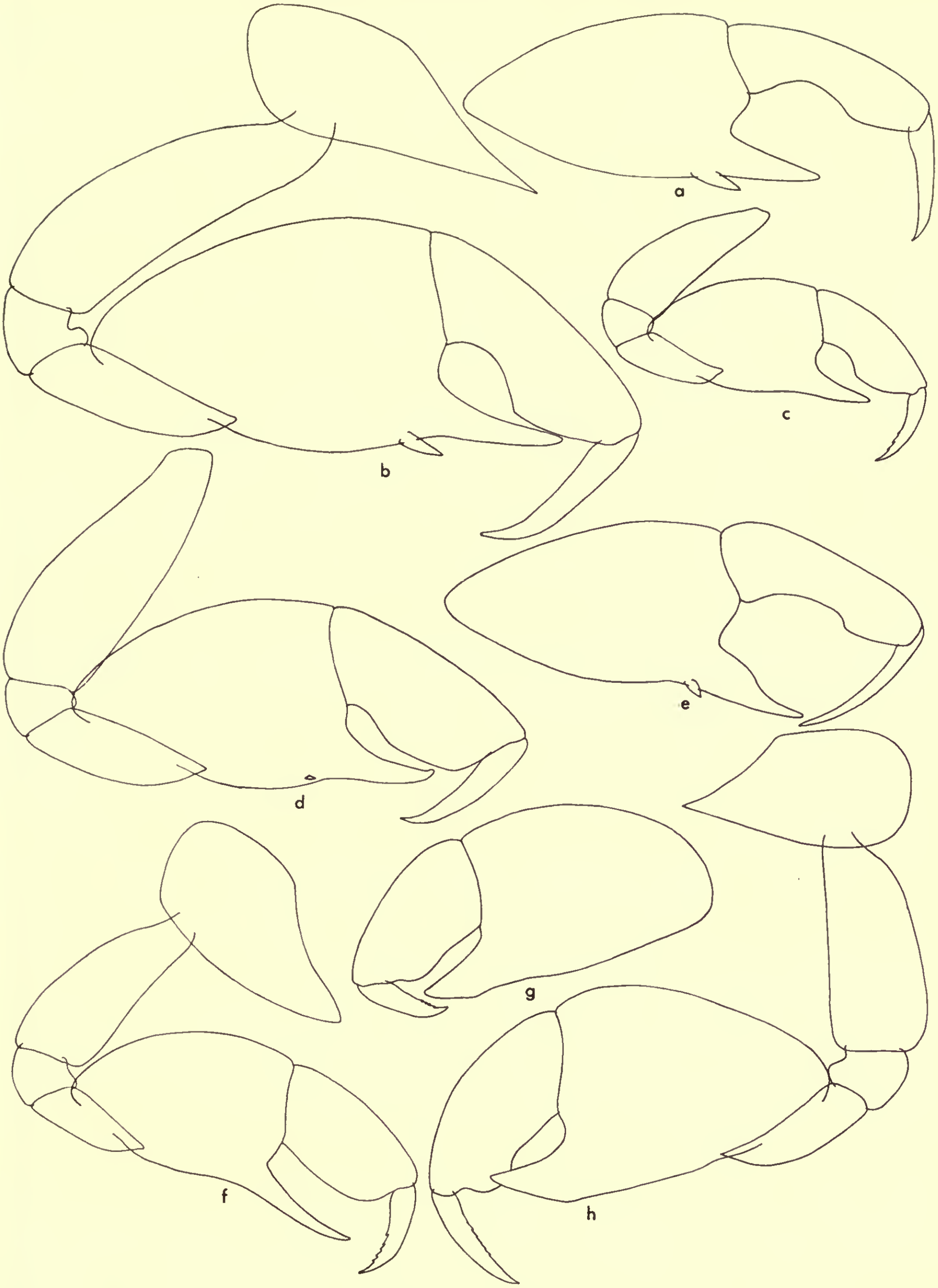

Fig. 8. *Microdeutopus anomalus* (Rathke). (a) Male gnathopod 1, Falmouth, Cornwall. (b) Male gnathopod 1, Bonifacio, Corsica. (c) Male gnathopod 1, Falmouth, Cornwall. (d) Male gnathopod 1, Isle of Mull, Scotland. (e) Male gnathopod 1, Isle of Mull, Scotland. *Microdeutopus damnoniensis* (Bate). (f) Male gnathopod 1, Plymouth, Devon. *Microdeutopus algicola* Della Valle. (g) Male gnathopod 1, Naples, Italy. (h) Male gnathopod 1, Bône, Algeria.

Fage, 1925). This has often led to the attributing of immature material of the present species to *M. damnoniensis* (Bate), the separation of which must be made with great care. In its immature form, or in mature specimens lacking an accessory tooth, *M. anomalus* is distinguishable from *M. algicola* Della Valle by the form of the primary tooth which arises at the posterior distal angle of article 5 and is relatively slender, though never as slender as in *M. damnoniensis*. In *M. algicola* (Text-figs, 8g–h) a considerable area of the posterior margin of article 5 contributes to the development of the tooth, which is hence very robust. *M. anomalus* differs from *M. damnoniensis* also in the form of the tooth on article 5 of gnathopod 1, but is more easily distinguished from that species by the structure of the second gnathopod, which is slender and elongate with an oblique palm in *M. anomalus* (Text-fig. 9c), relatively short and broad, with an almost transverse palm in *M. damnoniensis* (Text-fig. 9a). In addition, the rami of uropod 3 are long and slender in *M. anomalus* (Text-fig. 9e) ,whereas they are short and broad in *M. damnoniensis* (Text-fig. 9g).

ECOLOGY. A sub-littoral species in depths ranging down to 200 metres, but occasionally extending into the intertidal zone. In areas influenced by detritus, often among arborescent weeds, but also in *Zostera* beds, and among shells, polyzoans, sponges, tunicates and *Mytilus*. In the Black Sea, associated with *Modiola phaseolina* and *Amphiura florifera*.

DISTRIBUTION. Norway south of the Lofoten Islands, Sweden, Denmark, including the Baltic, the British Isles, particularly the South and West coasts, the channel coasts of France, including the Channel Islands, along the Atlantic coasts of France, Spain, Portugal and North West Africa to the Canary Isles. Throughout the Mediterranean, Adriatic, Aegean, Ionian and Black seas, in the Bermudas and on the north-eastern seaboard of the United States of America (Rhode Island and Massachusetts).

Microdeutopus damnoniensis (Bate)

(Text-figs. 7b, 8f, 9a, g, 10a–b, 20h, j)

Lembos damnoniensis Bate, 1856 (*nomen nudum*): 58; Bate, 1857 : 142.
Lembos danmoniensis [*sic*] (Bate) White, 1857 : 180.
Microdeutopus gryllotalpa Bate, 1862 : 163, pl. 30, fig. 1; Bate & Westwood, 1863 : 289.
Microdeutopus damnoniensis (Bate) Norman, 1905a : 24; Stebbing, 1906 (pro-parte) : 593; Chevreux & Fage, 1925 (pro-parte): 297, fig. 308; Barnard, 1958 : 29.
Microdeutopus danmoniensis [*sic*] (Bate) Norman & Scott, 1906: 83.
[Non] *Microdeutopus danmoniensis* [*sic*] Sars, 1894: 542, pl. 192.

TYPE LOCALITY. Plymouth, Devon, England.

DIAGNOSIS OF MALE. *Antennule* slightly over one half the body length, the first and second peduncular articles subequal, the third almost one half the length of the second; flagellum a little longer than the peduncle, normally with up to fourteen articles (maximum recorded fifteen); accessory flagellum with two articles the terminal article rudimentary. *Antenna* shorter than the antennule, the fourth and fifth peduncular articles subequal; flagellum about equal to the fifth peduncular article normally with up to seven articles (maximum recorded eight). *Peraeon* segments 2–4 each with an anteriorly directed spine in the mid-ventral line, that of segment 2 the longest. *Gnathopod* 1 with article 1 moderately produced anteriorly, less acute than in *M. anomalus* or *M. algicola*; article 2 expanded somewhat distally; article 5 very enlarged, longer than broad, the posterior distal angle produced into a single, long, slender, inward curved tooth which in fully mature specimens considerably exceeds half the length of article 6; article 6 with the posterior margin smoothly rounded; article 7 relatively long with accessory teeth on the posterior margin. *Gnathopod* 2 with article 2 expanded; articles 5 and 6 short, 5 slightly the longer, but scarcely broader than article 6, which is scarcely twice as long as broad, and has the palmar angle almost transverse; article 7 short and robust. *Uropod* 3 having the peduncle with its lateral and dorsal flanges very distinct, as in *M. algicola*; rami short and very stout, not exceeding the length of the peduncle, the exopodite the longer of the two rami, with two separated spines on the outer margin, the more distal of which is much the longer, endopodite with a single median spine on the outer margin, and a single more distal spine on the inner, each ramus terminating in a group of spines of which one is relatively long. *Telson* as *M. anomalus*.

Maximum size of male : 4·5 mm.

FEMALE. As the male, except for the structure of the sexually dimorphic gnathopoda, and the absence of ventral peraeon spines. *Gnathopod* 1 with article 1 not markedly produced anteriorly, very obtuse; article 2 somewhat expanded; article 6 slightly longer than article 5 and narrowing somewhat at the junction with it; article 7 longer than the palmar region. *Gnathopod* 2 with article 2 unexpanded and article 6 somewhat longer and more slender than article 5, with the palmar margin angular.

Maximum size of female : 4·5 mm.

DISCUSSION. Andersson (1954) using material of Swedish origin concluded that *M. propinquus* Sars and *M. damnoniensis* (Bate) were both synonyms of *M. anomalus* (Rathke). Present investigations, whilst supporting the contention that *M. propinquus* is synonymous with *M. anomalus*, indicate that *M. damnoniensis* certainly is not. Since there are no substantiated records of *M. damnoniensis* north of latitude 51° N. it is probable that Andersson was working entirely with a population of *M. anomalus*. The distinction between *M. anomalus* and *M. damnoniensis* is not simply one of presence or absence of an accessory tooth, and most so-called *M. damnoniensis* in the literature are in fact immature *M. anomalus*. Nevertheless, true *M. damnoniensis* does exist and males are distinguishable from those of *M. anomalus* and *M. algicola* by a number of important characters, including the very slender, inward curved tooth on article 5 of gnathopod 1 (Text-fig. 8f), the short, broad articles 5 and 6 of gnathopod 2 (Text-fig. 9a), and the short, robust uropod 3 rami (Text-fig. 9g). In addition, the number of articles to the accessory flagellum of the antennule remains constant from eclosion to maturity, in contrast with the condition in *M. anomalus* where the number of articles increases with age.

ECOLOGY. Unlike *M. anomalus*, the present species occurs most commonly in the intertidal zone, among sponges, polyzoans and corallines, especially in rock pools, or in the shallow sub-littoral.

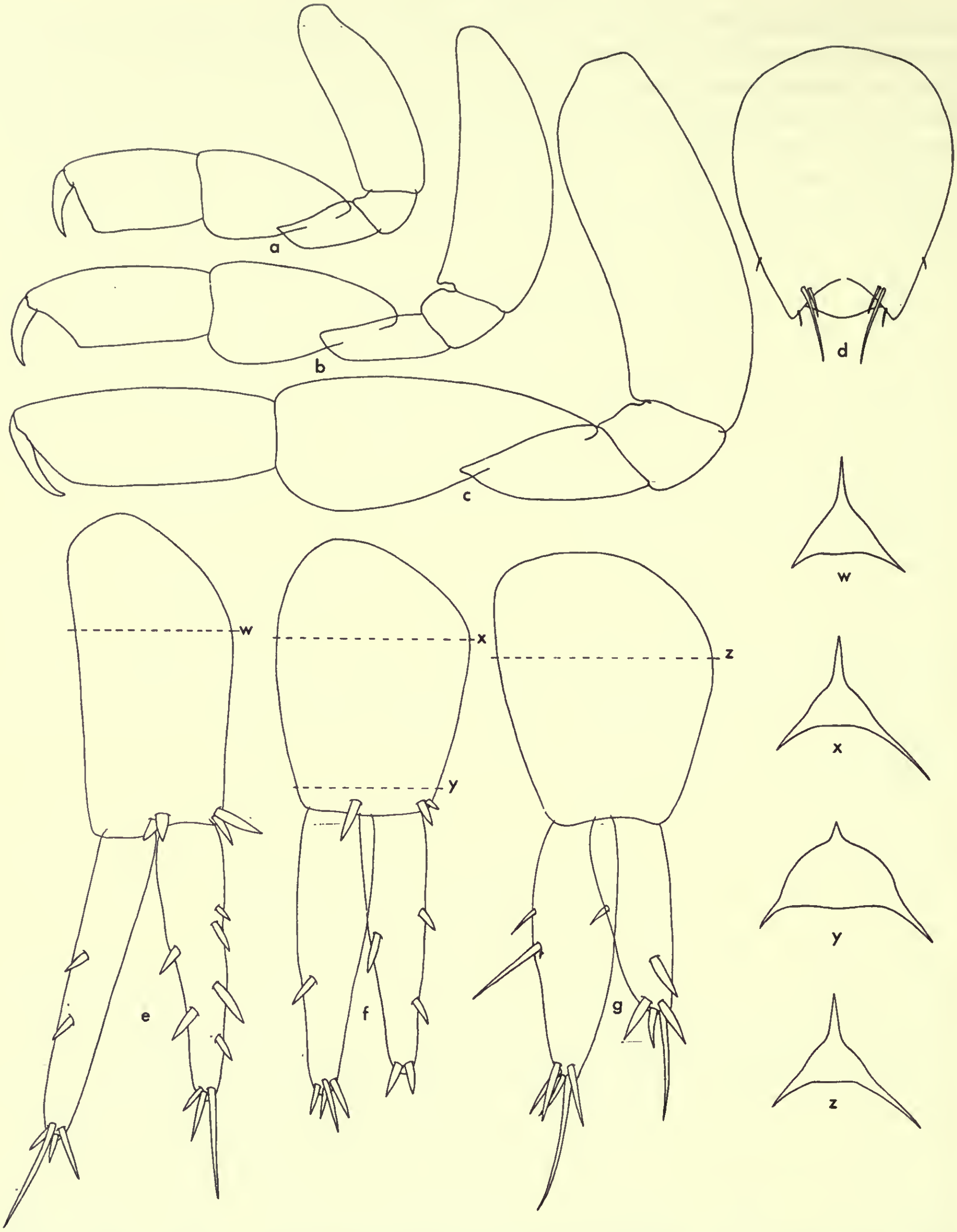

FIG. 9. *Microdeutopus damnoniensis* (Bate). (a) Male gnathopod 2, Plymouth, Devon. (g) Male uropod 3, with transverse section across peduncle at z, Plymouth, Devon. *Microdeutopus algicola* Della Valle. (b) Male gnathopod 2, Naples, Italy. (d) Male telson, Naples, Italy. (f) Male uropod 3, with transverse sections across peduncle at x and y, Naples, Italy. *Microdeutopus anomalus* (Rathke). (c) Male gnathopod 2, Plymouth, Devon. (e) Male uropod 3, with transverse section across peduncle at w, Plymouth, Devon.

DISTRIBUTION. Very difficult to ascertain, due to confusion in the literature with immature *M. anomalus*. Present investigations have confirmed material from Drake's Island and Wembury Bay, Plymouth, Jersey and Guernsey, and Bandol, France.

TYPE MATERIAL. A lectotype has been erected from Bate's syntypic series (see Appendix 2).

Microdeutopus algicola Della Valle

(Text-figs. 8g–h, 9b, d, f, 10d–e, 20f)

[?] *Microdeutopus grillotalpa* Sowinsky, 1880 : 125, pl. 5, fig. 17a–d.

Microdeutopus algicola Della Valle, 1893 : 418, pl. 1, fig. 3, pl. 11, figs. 1–12; Norman, 1905a : 25.

Microdeutopus damnoniensis (Bate) Stebbing, 1906 (pro-parte): 593; Chevreux & Fage, 1925 (pro-parte): 297, fig. 308; [?] Miloslavskaia, 1939a : 124, fig. 24; [?] Soika, 1949 : 199, [?] Gurjanova, 1951 : 834, fig. 584.

TYPE LOCALITY. Mergellina, Naples, Italy.

DIAGNOSIS OF MALE. Antennules and antennae have been missing in material examined in present investigations, and the description of these appendages here is extracted from the description and figures of Della Valle (1893). *Antennules* with the first and second peduncular articles sub-equal, the third about one third the length of the second; flagellum longer than the peduncle with twenty articles; accessory flagellum possibly with two articles, but almost certainly three, of which the terminal is rudimentary as figured (for *M. grillotalpa*) by Sowinsky (1880). *Antenna* shorter than the antennule, the fourth peduncular article slightly longer and more robust than the fifth, flagellum about equal to the fifth peduncular article, with eight articles. *Peraeon* segments 2–4 each with an anteriorly directed spine in the mid-ventral line, that of segment 2 the longest; segment 5 with a vestigial spine. *Gnathopod* 1 with article 1 moderately produced anteriorly, acute, though less attenuated than in *M. anomalus*; article 2 relatively robust, expanded somewhat distally; article 5 very enlarged, the posterior margin produced into a single, robust, broad based tooth not exceeding half the length of article 6; article 6 with the posterior margin convex distally, straight or slightly concave basally; article 7 robust, with accessory teeth on the posterior margin. *Gnathopod* 2 with article 2 having the anterior margin produced into a flange which terminates distally in a blunt process; articles 5 and 6 slender, subequal in length, article 5 slightly the broader; article 6 over twice as long as broad, with the palmar region oblique; article 7 short and robust. *Uropod* 3 with the peduncle broad, due to the marked development of the lateral flanges, particularly the inner, which exceeds in length both the outer flange and the dorsal crest; rami long and slender, about equal in length to the peduncle, the exopodite slightly the longer, not differing in spination from *M. anomalus* of a similar size. *Telson* as in *M. anomalus*.

Maximum size of male : 4·5 mm.

FEMALE. As the male, except for the structure of the sexually dimorphic gnathopoda, and absence of ventral peraeon spines. *Gnathopod* 1 with article 1 not markedly produced anteriorly, obtuse; article 2 robust, otherwise scarcely differing from that of *M. damnoniensis*. *Gnathopod* 2 with article 6 having the palmar angle rounded, otherwise as that of *M. damnoniensis*.

Maximum size of female 4·5 mm.

Discussion. *M. algicola* is the most robust member of the "*anomalus*" group of species. In facies it more closely resembles *M. stationis*, than it does *M. anomalus* or *M. damnoniensis*, and it is noteworthy that a male *M. algicola* was discovered during present re-examinations of *M. stationis* material in the Chevreux collections. Male *M. algicola* are distinguishable from those of *M. damnoniensis*, in having the tooth on article 5 of gnathopod 1 (Text-figs. 8g–h) broad-based and triangular, whereas in *M. damnoniensis* (Text-fig. 8f) it is slender throughout its length, arising

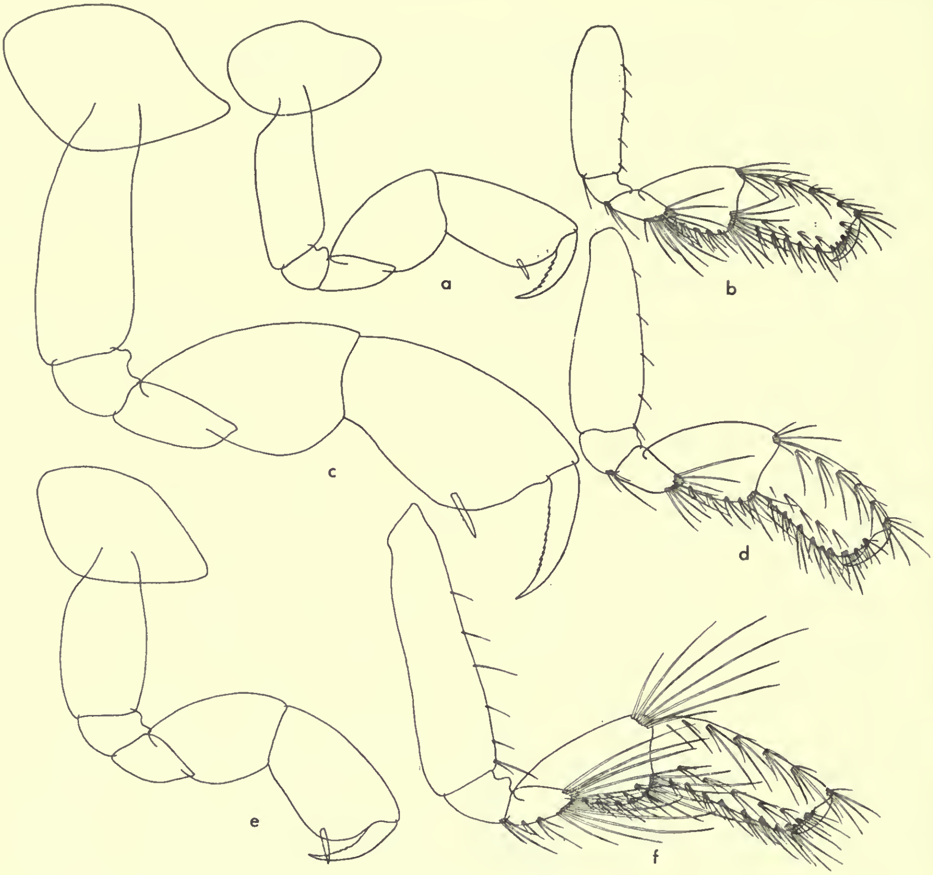

Fig. 10. *Microdeutopus damnoniensis* (Bate). (a) Female gnathopod 1, Plymouth, Devon. (b) Female gnathopod 2, Plymouth, Devon. *Microdeutopus anomalus* (Rathke). (c) Female gnathopod 1, Plymouth, Devon. (f) Female gnathopod 2, Plymouth, Devon. *Microdeutopus algicola* Della Valle. (d) Female gnathopod 2, Naples, Italy. (e) Female gnathopod 1, Naples, Italy.

at the posterior distal angle only. The present species also differs from *M. damnoniensis* in the structure of gnathopod 2 (Text-fig. 9b), which has articles 5 and 6 slender, as in *M. anomalus* and in the form of uropod 3 (Text-fig. 9f), which has slender elongate rami. In lacking an accessory tooth on article 5 of the male gnathopod 1, *M. algicola* differs from typical *M. anomalus* which usually possesses such a tooth. In specimens of the latter species lacking an accessory tooth (including immature specimens) the primary tooth is structurally very different, being longer and more slender, with the posterior margin more smoothly rounded, and with a narrower base, than it is in *M. algicola*. In addition, the flange on the anterior margin of article 2 of gnathopod 2 terminates distally in a more markedly developed process in *M. algicola* than in *M. anomalus*.

ECOLOGY. At Mergellina (Della Valle, 1893) among attached algae on the shore, and at Bône in 15–20 metre depth.

DISTRIBUTION. Difficult to ascertain, due to the scarcity of reliable records. The present author has seen material from Naples, Italy and Bône, Algeria, and considers that the *M. grillotalpa* Sowinsky from Sevastopol in the Black Sea, refers to this species. The species may prove to be widely distributed in the Mediterranean region, and Black Sea.

THE " SCHMITTI " GROUP OF SPECIES

The "*Schmitti*" group of species occurs over a wide geographical area, around both the Pacific and Atlantic coasts of the Americas. So far material has been examined from a number of isolated geographical localities, and regional morphological differences are difficult to assign to varietal, subspecific and specific status. Nevertheless there seems at present to be justification for grouping these forms into at least three species, of which *M. schmitti* Shoemaker and *M. hancocki* Myers are sympatric, overlapping in their distribution and maintaining their separate identities. It is clear that ecological studies on the "*schmitti*" group of species would be of considerable value.

Males of the "*schmitti*" group, with the exception of *M. schmitti* itself, differ from those of all other species of *Microdeutopus* by the development of a tooth on the anterior margin of article 5 of gnathopod 1. *M. schmitti* differs from *M. gryllotalpa* Costa (the only species with which it could be confused) by having article 2 of gnathopod 2 concave and smooth on the anterior margin, whereas in *M. gryllotalpa* the anterior margin is convex and crenated. Females of *M. schmitti* differ from those of all other known species in the genus (but see also *Hansenella longicornis* Chevreux, p. 138) by the development of a tooth or teeth on the posterior margin of article 5 of gnathopod 1. Females of other species in the "*schmitti*" group are without recognizable diagnostic features and their identification in the absence of males cannot be attempted with certainty. Most apparent differences in structure between *M. schmitti* and the smaller species *M. hancocki* and *M. trichopus* are due to neoteny. The rami of the third uropod of mature female *M. hancocki* and *M. trichopus*, for example, correspond to those of immature specimens of *M. schmitti* of a similar size.

Microdeutopus schmitti Shoemaker

(Text-figs. 11, 13b, d, 14a–c, f, g, l, 15, 16a–b, d, 20m, pl. 1b)

Microdeutopus schmitti Shoemaker, 1942 : 18, fig. 6; Barnard, 1958 : 29; Barnard, 1959 : 32, pl. 9; Myers, 1968b : in press.

TYPE LOCALITY. Bahia de Magdalena, Baja California, Mexico.

DIAGNOSIS OF MALE. *Paragnaths* with the mandibular processes relatively short and stout. *Antennule* slightly over one third the body length, the first and second peduncular articles subequal, the third a little less than one half the length of the second; flagellum about equal in length to the peduncle, normally with up to ten articles (maximum recorded twelve); accessory flagellum with three articles, the third article rudimentary. *Antenna* about two thirds the length of the antennule, the fourth and fifth peduncular articles subequal; flagellum shorter than the fifth peduncular article, with four articles, of which the first is equal to the combined length of the terminal three. *Peraeon* segments 3–6 each with a short, robust,

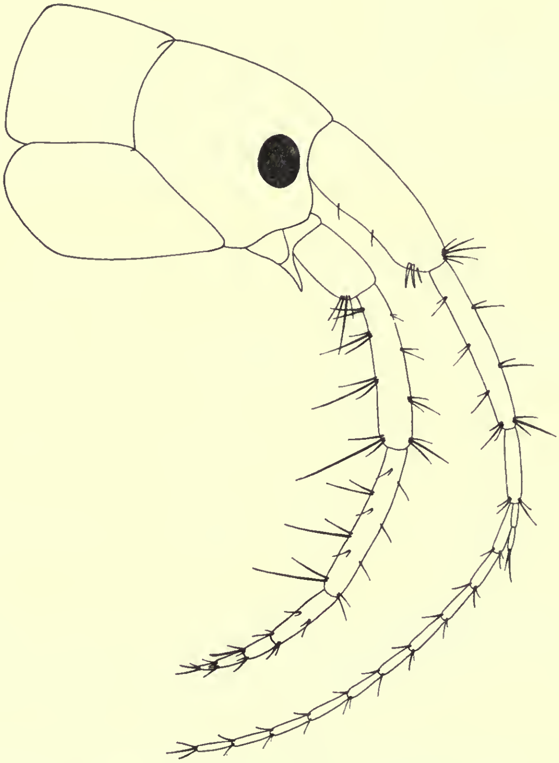

FIG. 11. *Microdeutopus schmitti* Shoemaker. Male head, Bahia de Salinas, Costa Rica.

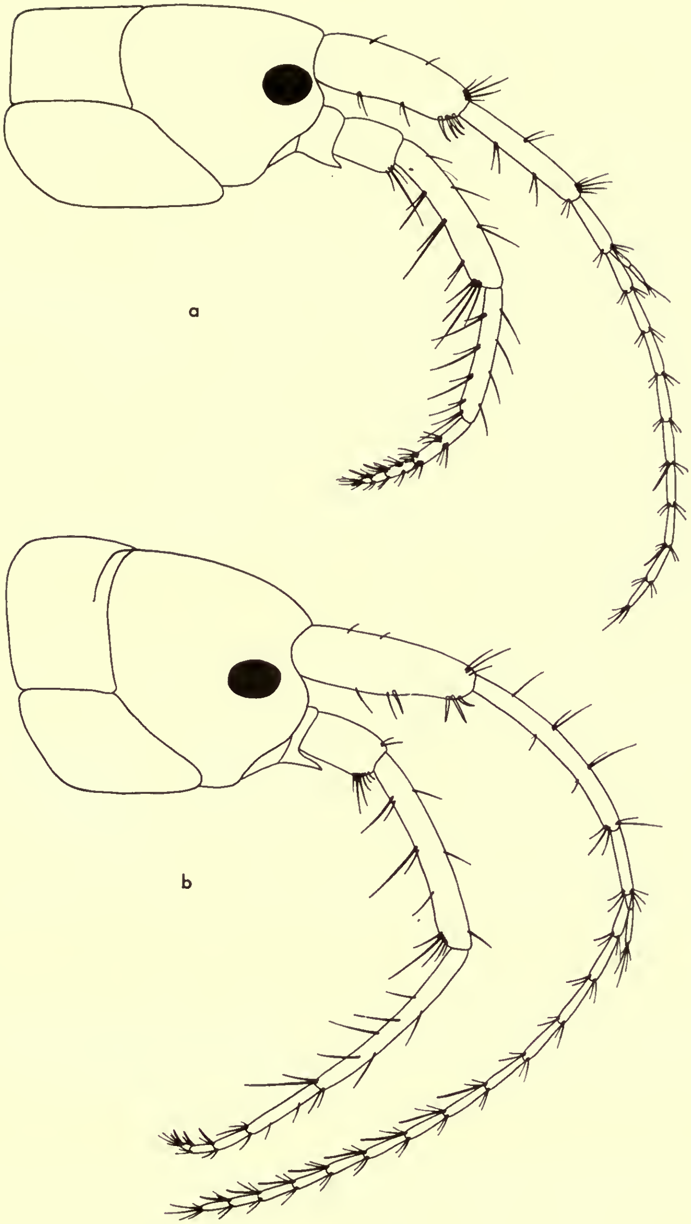

FIG. 12. *Microdeutopus hancocki* Myers. (a) Male head, Bahia de Salinas, Costa Rica (Paratype). *Microdeutopus trichopus* Myers. (b) Male head, Isabela Island, Galapagos (Paratype).

anteriorly directed spine in the mid-ventral line. *Gnathopod* 1 with article 1 moderately produced anteriorly, rounded; article 2 expanded, oval, article 4 roughly triangular, with relatively short setae on the posterior margin; article 5 longer than broad, without teeth on the anterior margin, the posterior distal angle produced into a large, stout tooth, at the base of which are from one to four small forward projecting teeth; article 6 short, the posterior margin with a distal and proximal lobe; article 7 relatively long, with accessory teeth on its posterior edge. *Gnathopod* 2 with article 2 somewhat concave on its anterior margin, the anterior distal corner produced into a rounded lobe; article 5 slightly longer than article 6 and expanded distally, where it considerably exceeds the width of article 6; articles 4, and 5 with numerous long, finely pectinate setae arising from the anterior and posterior margins. *Uropod* 3 with the rami subequal, slightly longer than the peduncle; endopodite with two to four equally spaced spines on the inner margin and one or two on the outer; exopodite with two well separated spines on the inner margin, and on the outer a solitary spine, basal to which in fully mature adults is a pair of closely associated spines, the outer of which is the longer. *Telson* with each terminal crest bearing on its distal dorsal margin a group of three or four setae, two or three of which are short and spiniform. Additional setae may appear spiniform during growth, which is in contrast with the condition in *M. stationis* where the spines are always quite distinct from the setae.

Maximum size of male : 5 mm.

FEMALE. As the male except for the absence of ventral peraeon spines, and the sexually dimorphic gnathopoda. *Gnathopod* 1 with article 2 unexpanded; articles 5 and 6 subequal in length, article 5 distinctly the broader, with the posterior distal angle produced into one or two small teeth, article 6 with the anterior margins roughly parallel; article 7 slender, considerably longer than the palmar region with accessory teeth on the posterior edge. *Gnathopod* 2 with article 2 unexpanded; articles 5 and 6 subequal in length, article 5 roughly pentagonal with the anterior margin almost straight, broadening distally, where it considerably exceeds the breadth of article 6; anterior and posterior margins of articles 4 and 5 bearing long pectinate setae.

Maximum size of female : 6 mm.

DISCUSSION. *M. schmitti* is closely related to *M. hancocki* and *M. trichopus* but differs from these in the male, by having the anterior margin of article 5 of gnathopod 1 (Text-figs. 13b, d) devoid of any toothlike processes and in the female by the presence of teeth on the posterior distal angle of article 5 of gnathopod 1 (Text-fig. 16b, d).

ECOLOGY. In the sub-littoral to a recorded depth of 42 metres (off Point Loma Light, California). Tolerant of a wide range of conditions, on mud, fine or course sand, and rock substrata, among various vegetation, shells, and coral.

DISTRIBUTION (Text-fig. 15). Along the coasts of California (Cayucos, Point Conception, Point Loma, San Clemente, and Newport), Baja California (El Coyote, Bahia de San Quintin, Bahia de Magdalena and Cape San Lucas) and Costa Rica (South Viradores Islands, Playa Blanca and Bahia de Salinas).

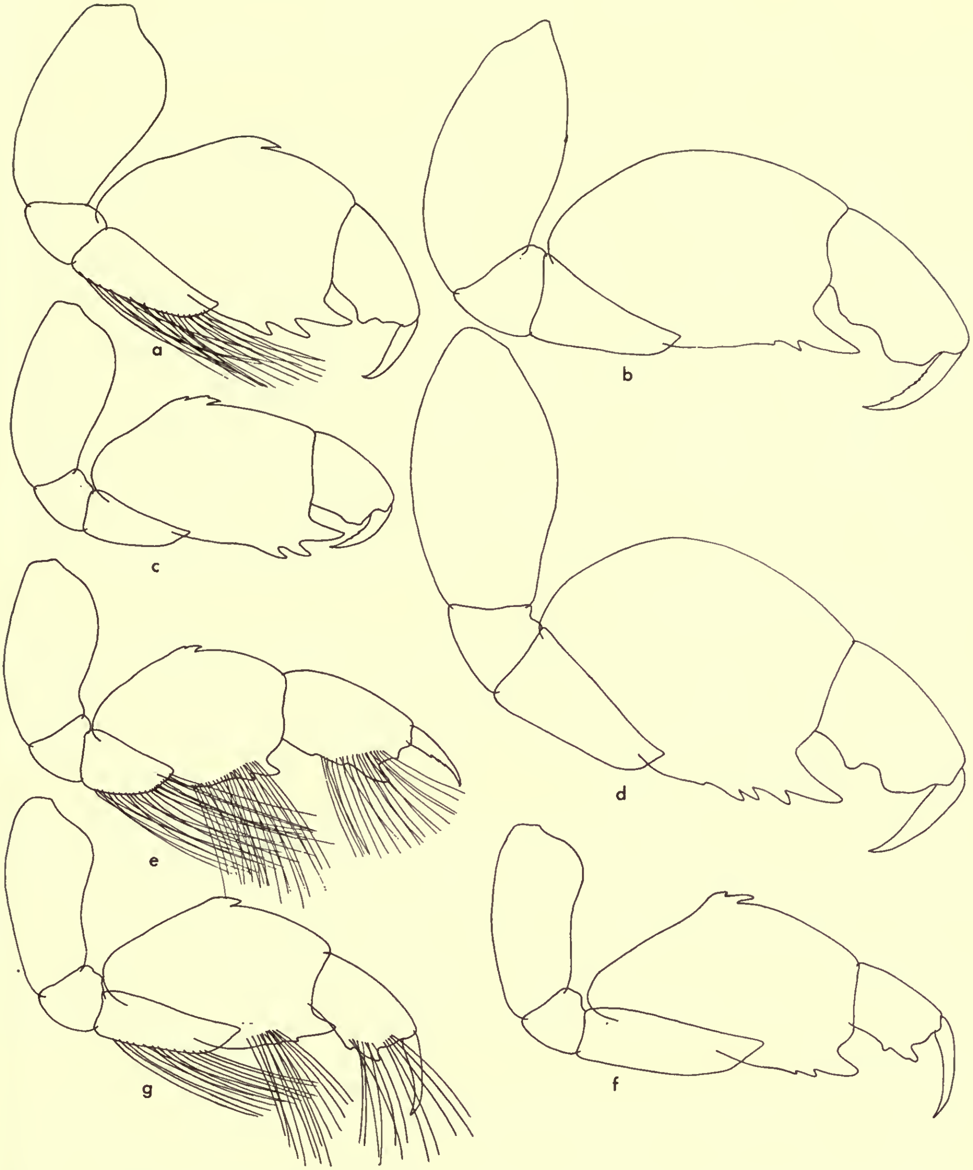

FIG. 13. *Microdeutopus hancocki* Myers. (a) Male gnathopod 1, Bahia de Salinas, Costa Rica (Holotype). (c) Male gnathopod 1, Salango Island, Equador. *Microdeutopus schmitti* Shoemaker. (b) Male gnathopod 1, Bahia de San Quintin, Baja California. (d) Male gnathopod 1, Bahia de Salinas, Costa Rica. *Microdeutopus trichopus* Myers. (e) Male gnathopod 1, Isabela Island, Galapagos (Holotype). *Microdeutopus* sp. nov.? (f) Male gnathopod 1, Tortugas, Florida, U.S.A. (g) Male gnathopod 1, Tortugas, Florida, U.S.A.

Microdeutopus hancocki Myers

(Text-figs. 12a, 13a, c, 14d, h, m, 15, 16c, e, 20k, pl. 1a)

Microdeutopus hancocki Myers, 1968b : In press.

TYPE LOCALITY. Bahia de Salinas, Costa Rica.

DIAGNOSIS OF MALE. *Antennules* and *antennae* not noticably different from those of *M. schmitti*. *Paragnaths* with the mandibular processes longer and more slender than in *M. schmitti*. *Peraeon* segments 3–5 each with a short robust, anteriorly directed spine in the mid-ventral line, segment 6 with a small or vestigial spine. *Gnathopod* 1 with article 1 moderately produced anteriorly, rounded; article 2 markedly expanded anteroproximally; article 4 roughly triangular, with very long setae on the posterior margin; article 5 longer than broad, oval, with a median dentiform process on the anterior margin, and at the posterior distal angle, three stout teeth, the most distal of which is the longest; article 6 short, with a single lobe on the posterior margin; article 7 relatively long, with accessory teeth on the posterior edge. *Gnathopod* 2 with article 2 concave on the anterior margin; article 5 considerably longer than article 6 but scarcely broader; articles 4 and 5 with numerous long, finely pectinate setae arising from the anterior and posterior margins. *Uropod* 3 and *telson* scarcely differing from those of *M. schmitti* of a comparable size.

Maximum size of male 3·8 mm.

FEMALE. As the male except for the absence of ventral peraeon spines, and the sexually dimorphic gnathopoda. *Gnathopod* 1 similar to that of *M. schmitti* but with the posterior margin of article 5 without teeth at the posterior distal angle. *Gnathopod* 2 scarcely differing from that of *M. schmitti*, but with the pentagonal shape of article 5 less well marked.

Maximum size of female 4·1 mm.

DISCUSSION. *M. hancocki* is very closely related to *M. schmitti*, from which it differs in the male having a tooth-like process on the anterior margin of article 5 of gnathopod 1 (Text-fig. 13a, c), and article 4 of this appendage bearing very long setae. In addition the structure of the ventral peraeon spines (Text-fig. 20k) and paragnath (Pl. 1a) and the shape of the second gnathopod (Text-fig. 14m) distinguishes the present species from *M. schmitti*. It differs from *M. trichopus* by having article 6 of gnathopod 1 devoid of any forward projecting teeth on its posterior margin.

ECOLOGY. Apparently more habitat-specific than *M. schmitti*, having been recorded at present only from sandy bottoms to a depth of about 18 metres.

DISTRIBUTION (Text-fig. 15). Costa Rica (Bahia de Salinas), Panama (Bahia Honda), Equador (Salango Island), and Galapagos (Isabela Island).

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crest of male telson, Bahia de Salinas, Costa Rica (Paratype). (m) Male gnathopod 2, Bahia de Salinas, Costa Rica (Paratype). *Microdeutopus trichopus* Myers.(e) Male uropod 3, Isabela Island, Galapagos (Holotype). (i) Dorsal view of left terminal crest of male telson, Isabela Island, Galapagos (Holotype). (j) Male gnathopod 2, Isabela Island, Galapagos (Paratype). *Microdeutopus* sp. nov.? (k) Male gnathopod 2, Tortugas, Florida.

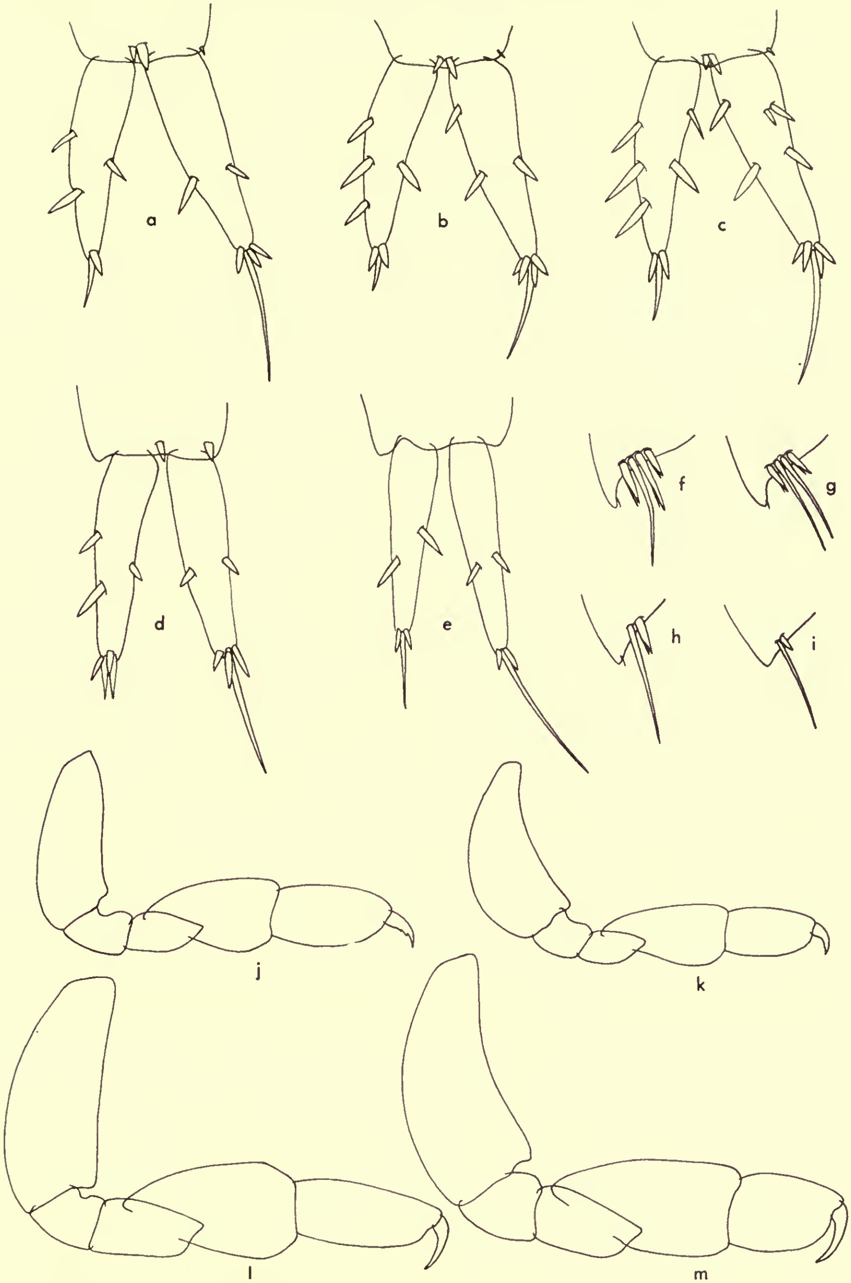

FIG. 14. *Microdeutopus schmitti* Shoemaker. (a)–(c) Male uropod 3, all figured the same size (and therefore each at a different scale) for easy comparison. (a) 3·0 mm. ♂ (b) 4·5 mm ♂ (c) 5·0 mm. ♂, Bahia de San Quintin, Baja California. (f) (g) Dorsal view of left terminal crest of male telson, Bahia de San Quintin, Baja California. (l) Male gnathopod 2, Bahia de San Quintin, Baja California. *Microdeutopus hancocki* Myers. (d) Male uropod 3, Bahia de Salinas, Costa Rica (Holotype). (h) Dorsal view of left terminal

Microdeutopus trichopus Myers

(Text-figs. 12b, 13e, 14e, i, j, 15, 16f–g, 20g)

Microdeutopus trichopus Myers, 1968b : In press.

TYPE LOCALITY. East of south end of Isabela Island, Galapagos.

DIAGNOSIS OF MALE. *Antennule* slightly over one half the body length, the first peduncular article slightly shorter than the very slender second article, the third about a third the length of the second article; flagellum somewhat longer than the peduncle, normally with up to twelve articles (maximum recorded thirteen); accessory flagellum with three articles, the third rudimentary. *Antenna* about two thirds the length of the antennule, the fourth and fifth peduncular articles elongate, slender subequal; flagellum shorter than the fifth peduncular article with four, rarely five articles, the first article long, about equal to the combined length of the terminal three or four. *Peraeon* segments 3–6 each with a long and slender spine in the mid-ventral line, those of segments 3 and 4 directed anteriorly those of segments 5 and 6 straight or slightly recurved. *Gnathopod* 1 with article 1 moderately produced anteriorly, rounded; article 2 expanded anteroproximally; article 4 short and bulky; article 5 oval, longer than broad, with a median dentiform process on the anterior margin and at the posterior distal angle, a short stout tooth, basal to which on the posterior margin is a further small tooth; article 6 over one half the length of article 5, the palmar angle produced into a short, blunt ending, forwardly projecting tooth, opposable to article 7; article 7 of moderate length, with accessory teeth on the posterior margin; the posterior margins of articles 4, 5 and 6 densely setose, the setae exceptionally long, in the largest males measuring 0·5 mm., 0·4 mm. and 0·3 mm. on each article respectively. *Gnathopod* 2 with article 2 somewhat expanded distally, the anterior margin slightly concave; articles 5 and 6 subequal in length, article 5 slightly the broader. *Uropod* 3 with the rami long and slender, longer than the peduncle, the exopodite slightly the longer of the two rami; each ramus with a single spine on each of the inner and outer margins. *Telson* with each terminal crest bearing on its distal dorsal margin a long seta and a short stout spine.

Maximum size of male : 3·8 mm.

FEMALE. As the male except for the absence of ventral peraeon spines, and sexually dimorphic gnathopoda. *Gnathopod* 1 with article 2 unexpanded, articles 5 and 6 slender, subequal in length, article 6 somewhat broader distally than at the junction with article 5; article 5 without teeth at the posterior distal angle; article 7 longer than the palmar region, with accessory teeth on the posterior edge. *Gnathopod* 2 with article 2 unexpanded; articles 5 and 6 subequal in breadth, article 6 slightly the longer, broadening distally; article 7 short and stout.

Maximum size of female: 4·0 mm.

DISCUSSION. *M. trichopus* differs in the male from all other known *Microdeutopus* species (but see following form and *Lembopsis* Pearse, (p. 139), in having the posterior margin of article 6 of gnathopod 1 (Text-fig. 13c) produced into a forward projecting tooth opposable to article 7.

ECOLOGY. *M. trichopus* appears to be a relatively deep water species having been absent from samples of *M. hancocki* taken in shallow waters in geographical areas where the present species is known to occur. Recorded from 58–110 metres over mud, and also among nullipores on sandy bottoms.

DISTRIBUTION. Galapagos (two localities off Isabella Island).

Microdeutopus sp. nov.?

(Text-figs. 13f–g. 14k, 15, 20)

Two males and a single female of a species of *Microdeutopus* of the "*schmitti*" group, were examined, from Tortugas, Florida. This material most closely resembles *M. trichopus* from the Galapagos archipelago but it differs from that species particularly in the structure of the male gnathopod 1. This has article 4 elongate and rectangular in the present material, whereas it is short and triangular in *M. trichopus*, in addition article 6 is short and article 7 opposable to the teeth of both articles 5 and 6 in present material, whereas in *M. trichopus* article 6 is over half the length of the article 5, with article 7 opposable to the teeth of article 6 only. Lastly, the setation of gnathopod 1 is considerably more sparse in present material than in *M. trichopus*. On gnathopod 2 article 5 is slightly longer than article 6 in present material, whilst the same two articles are subequal in *M. trichopus*.

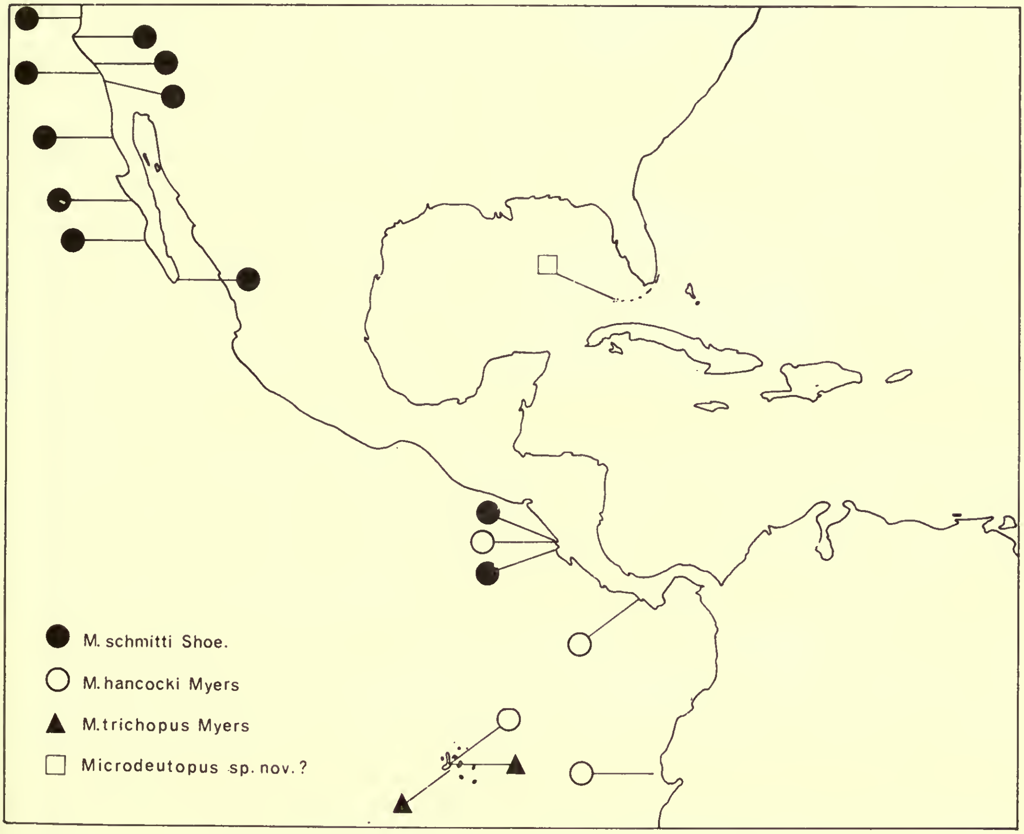

FIG. 15. The recorded distribution of the "*schmitti*" group of species in the Americas.

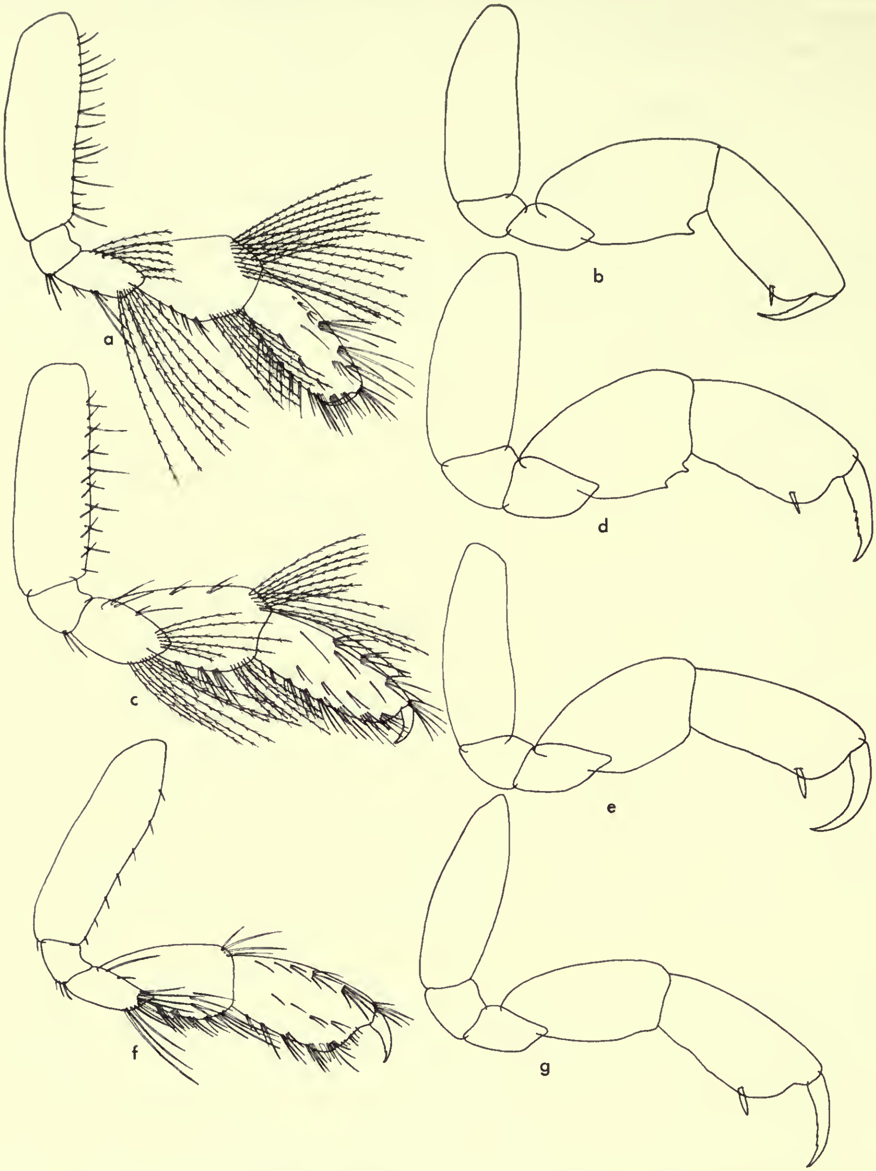

Fig. 16. *Microdeutopus schmitti Shoemaker.* (a) Female gnathopod 2, Bahia de San Quintin, Baja California. (b) Female gnathopod 1, Bahia de San Quintin, Baja California. (d) Female gnathopod 1, Bahia de Salinas, Costa Rica. *Microdeutopus hancocki* Myers. (c) Female gnathopod 2, Bahia Honda, Panama (Paratype). (e) Female gnathopod 1, Bahia Honda, Panama (Paratype). *Microdeutopus trichopus* Myers. (f) Female gnathopod 2, Isabela Island, Galapagos (Paratype). (g) Female gnathopod 1, Isabela Island, Galapagos (Paratype).

The present form is separated geographically from *M. trichopus* by the Central American isthmus, which has not been severed since the late Miocene, so one might expect the two forms to be specifically distinct. This possibility is strengthened by what is known so far of the ecology of the two forms, *M. trichopus* occurring in, and apparently restricted to, muddy and sandy bottoms in over 50 metres depth, while present material is found in relatively shallow waters amongst weeds.

More abundant material from a wider range of localities is required before the true taxonomic status of the present form can be elucidated.

Description of male. *Antennules* and *antennae* missing. *Peraeon* segments 3–6 each with a spine on the mid-ventral line, those of segments 3 and 4 directed anteriorly, those of segments 5 and 6 straight or slightly recurved. *Gnathopod* 1 with article 1 moderately produced anteriorly, rounded; article 2 markedly expanded anteroproximally; article 4 very elongate, roughly rectangular; article 5 oval, longer than broad, with a median dentiform process on the anterior margin, and at the posterior distal angle, a short stout tooth, basal to which, on the posterior margin, are two further small teeth; article 6 about one third the length of article 5, the palmar angle produced into a short, blunt ending, irregular, forward projecting tooth, basal to which is a small lateral projection; article 7 relatively long, opposable to the teeth of both articles 5 and 6; the posterior margins of articles 4, 5, and 6 bearing long setae. *Gnathopod* 2 with article 2 very slender basally, markedly expanded proximally; article 5 somewhat longer and broader than article 6. *Uropod* 3 with the rami long and slender, longer than the peduncle, the exopodite the longer of the two rami, each ramus with a single spine on its inner margin. *Telson* with each terminal crest bearing on its distal dorsal margin, a long seta, and a short spine.

Length of males : 3·4 mm. and 3·5 mm.

Female. *Antennules* missing. *Antennae* about one third the body length, the fourth and fifth peduncular articles elongate, slender, subequal; flagellum shorter than the fifth peduncular article, with four articles, the first article long, slightly shorter than the combined length of the terminal three. *Gnathopods* 1 and 2 not differing from those of *M. trichopus*.

Length of female : 3·3 mm.

Material. 1 ♂ and 1 ♀; station 48–30, 9th August, 1930, east and south of Loggerhead Light, Dry Tortugas, Monroe Co., Florida, in 20–20 metres. 1 ♂; station 12–31, 26th June, 1931, Tortugas, Florida (24° 36′ N. 82° 56′ W. approx. from chart) in 18–20 metres (low water) net tow-weedy haul.

Microdeutopus armatus Chevreux

(Text-figs. 17d, 18, 20l)

Microdeutopus armatus Chevreux, 1886 : XLI; Chevreux, 1887b : 312, pl. 5, figs. 11–12; Chevreux, 1887a : 92; Stebbing, 1906 : 589; Chevreux & Fage, 1925 : 296, figs. 303, 307; Barnard, 1958 : 29.

Stimpsonella armata (Chevreux) Della Valle, 1893 : 422, pl. 4, fig. 8, pl. 11 figs. 13–24; Chevreux, 1900 : 89; Norman 1905a : 25.

Type locality. North East of Basse-Kikerie, France.

Diagnosis of male. *Antennule* between one half and two thirds the body length, the second peduncular article longer than the first, the third a little over one third the length of the second; flagellum longer than the peduncle, normally with up to fourteen articles (maximum recorded sixteen); accessory flagellum with two articles,

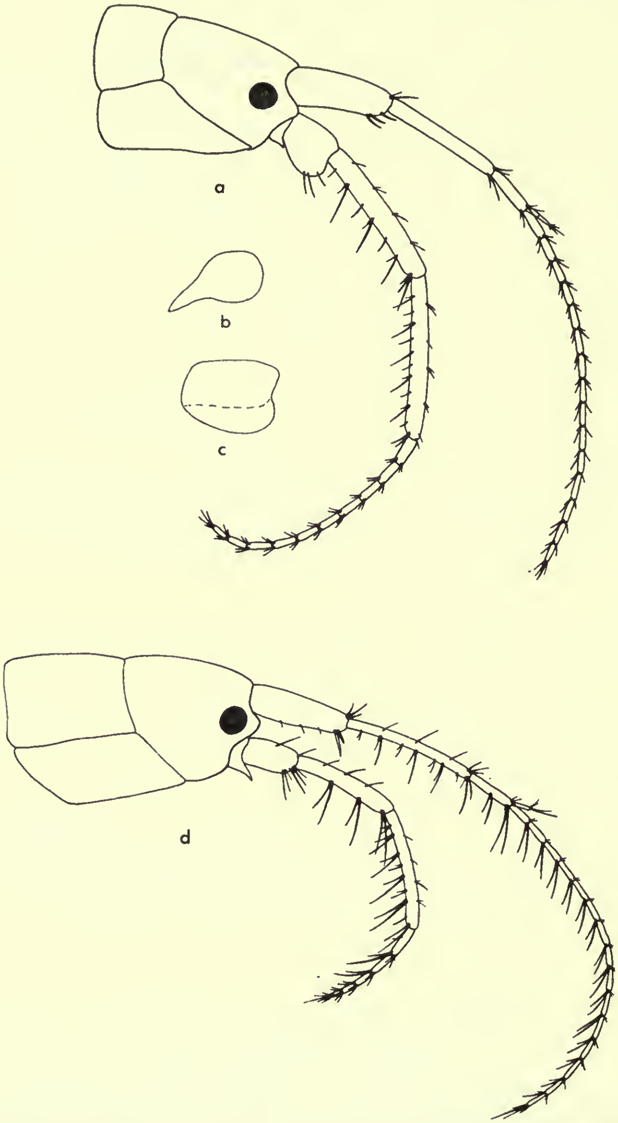

Fig. 17. *Microdeutopus chelifer* (Bate). (a) Male head, with (b) a transverse section and (c) a lateral view of the third peduncular article of the antenna, Jersey, Channel Islands. *Microdeutopus armatus* Chevreaux. (d) Male head, Villefranche, France.

the second article rudimentary. *Antenna* about two thirds the length of the antennule, the fourth and fifth peduncular articles subequal; flagellum slightly shorter than the fifth peduncular article with five articles. *Peraeon* segments 2–5 each with a spine in the mid-ventral line, that of segment 2 slender hook-shaped, directed anteriorly, those of segments 3–5 robust anteriorly directed, that of segment 5 the shortest. *Gnathopod* 1 with article 1 moderately produced anteriorly, acute; article 2 short and greatly expanded; article 5 almost as broad as long, the posterior distal angle produced into a large, broad, blunt ended tooth; article 6 short, the posterior margin irregularly lobed; article 7 relatively long. *Gnathopod* 2 with article 2 expanded, the anterior margin produced into a crenated flange; articles 5 and 6 roughly rectangular, subequal in length and breadth, article 6 with the palmar angle produced into a short tooth. *Uropod* 3 with the rami subequal, slightly shorter than the peduncle; endopodite with a pair of spines on the inner dorsal margin near the apex, and one long and one short terminal seta, exopodite with a similar pair of terminal setae. *Telson* with each terminal crest bearing, on its distal dorsal margin, a long seta.

Maximum size of male : 3 mm.

FEMALE. As the male except for the structure of the sexually dimorphic gnathopoda, and absence of ventral peraeon spines. *Gnathopod* 1 with article 2 somewhat dilated; article 6 longer than article 5, with the anterior and posterior margins roughly parallel, article 7 very elongate, exceeding in length the palmar region. *Gnathopod* 2 with article 2 expanded, the antero-distal corner produced into a lobe; article 6 considerably longer than article 5, with the palmar angle produced into a broad-based triangular process.

Maximum size of female : 4 mm.

DISCUSSION. *M. armatus* differs in the male from all other species in the genus, except *M. chelifer*, in having the second gnathopod chelate. It differs from the latter species by having the fifth and sixth articles of gnathopod 2 (Text-fig. 18d), subequal in length and breadth, whereas in *M. chelifer* (Text-fig. 19c), article 6 is much shorter and much broader than article 5. There is no justification for placing these two species together in a distinct genus (*Stimpsonella* Della Valle) as suggested by Della Valle (1893) on the basis of the chelate male second gnathopoda, since in other respects they exhibit no greater affinity with each other than they do with other *Microdeutopus* species. The most generally useful character enabling the identification of females of *M. armatus* is the structure of the second gnathopod (Text-fig. 18e), which has a pronounced projection at the antero-distal corner of article 2, and a triangular process at the palmar angle of article 6. In addition article 2 of the first gnathopod (Text-fig. 18a) is somewhat dilated.

ECOLOGY. On soft grey mud (type locality), fine or coarse sands, in the sublittoral, in 10–90 metres. At Naples (Della Valle, 1893), associated with *Urothoe* and *Ampelisca*.

DISTRIBUTION. France, from the type locality, southwards along the coasts of the Bay of Biscay (Le Croisic, Gulf of Gascony), Portugal, and in the Mediterranean off the coasts of France (Antibes, Villefranche) Corsica (Bonifacio) and Italy (Naples).

Microdeutopus chelifer (Bate)

(Text-figs. 17a–c, 19, 20n)

Stimpsonia chelifera Bate, 1862 : 162, pl. 29, fig. 9; Bate & Westwood, 1863 : 285; Stebbing, 1878 : 34, pl. 5, figs. 2–3; Norman, 1886 : 17.

Microdeutopus chelifer (Bate) Stebbing, 1888 : 334; Stebbing, 1906 : 589; Chevreux & Fage, 1925 : 295, fig. 306; Barnard, 1958 : 29.

[*Non*] *Microdeutopus chelifer* Haswell, 1879 : 340, pl. 22, fig. 3.

Stimpsonella chelifera (Bate) Della Valle, 1893 : 424, pl. 56, figs. 42–45; Norman, 1905a : 25; Norman, 1905b : 82; Norman & Scott, 1906 : 84; Norman, 1907 : 368.

TYPE LOCALITY. Salcombe, Devon, England.

DIAGNOSIS OF MALE. *Antennule* slightly over one half the body length, the second peduncular article a little longer than the first, the third over one third the length of the second; flagellum longer than the peduncle, normally with up to fifteen articles (maximum recorded seventeen); accessory flagellum with three articles, the third

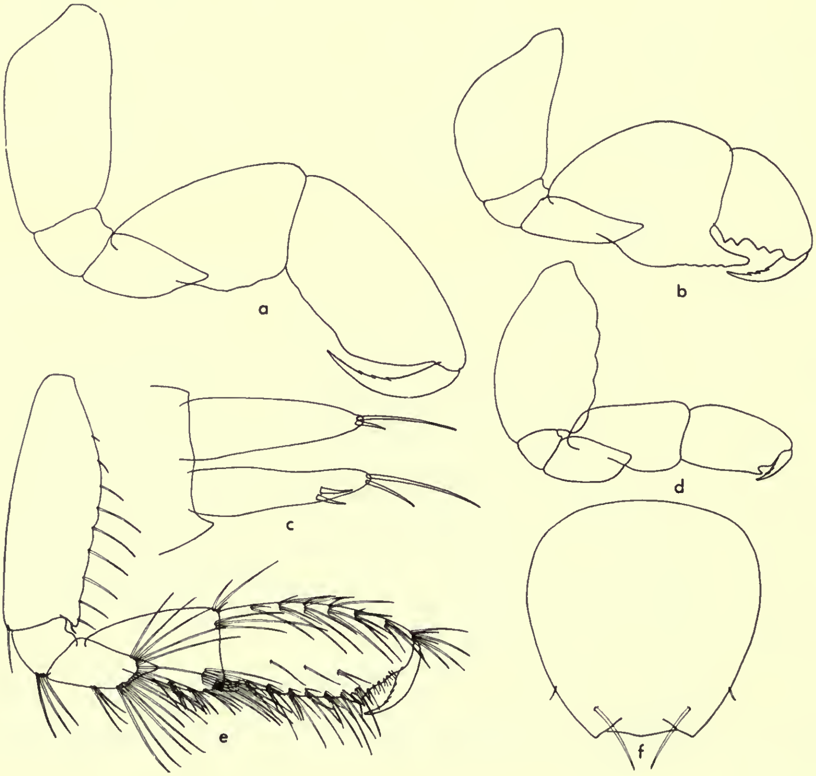

FIG. 18. *Microdeutopus armatus* Chevreux. (a) Female gnathopod 1, Le Croisic, France. (b) Male gnathopod 1, Le Croisic, France. (c) Male uropod 3, Le Croisic, France. (d) Male gnathopod 2, Le Croisic, France. (e) Female gnathopod 2, Le Croisic, France. (f) Male telson, Le Croisic, France.

article rudimentary. *Antenna* longer than the antennule, the third peduncular article with its lower outer margin produced into a flattened lobe, the fourth peduncular article very slightly shorter than the fifth; flagellum longer than the fifth peduncular article, normally with up to ten articles (maximum recorded eleven).

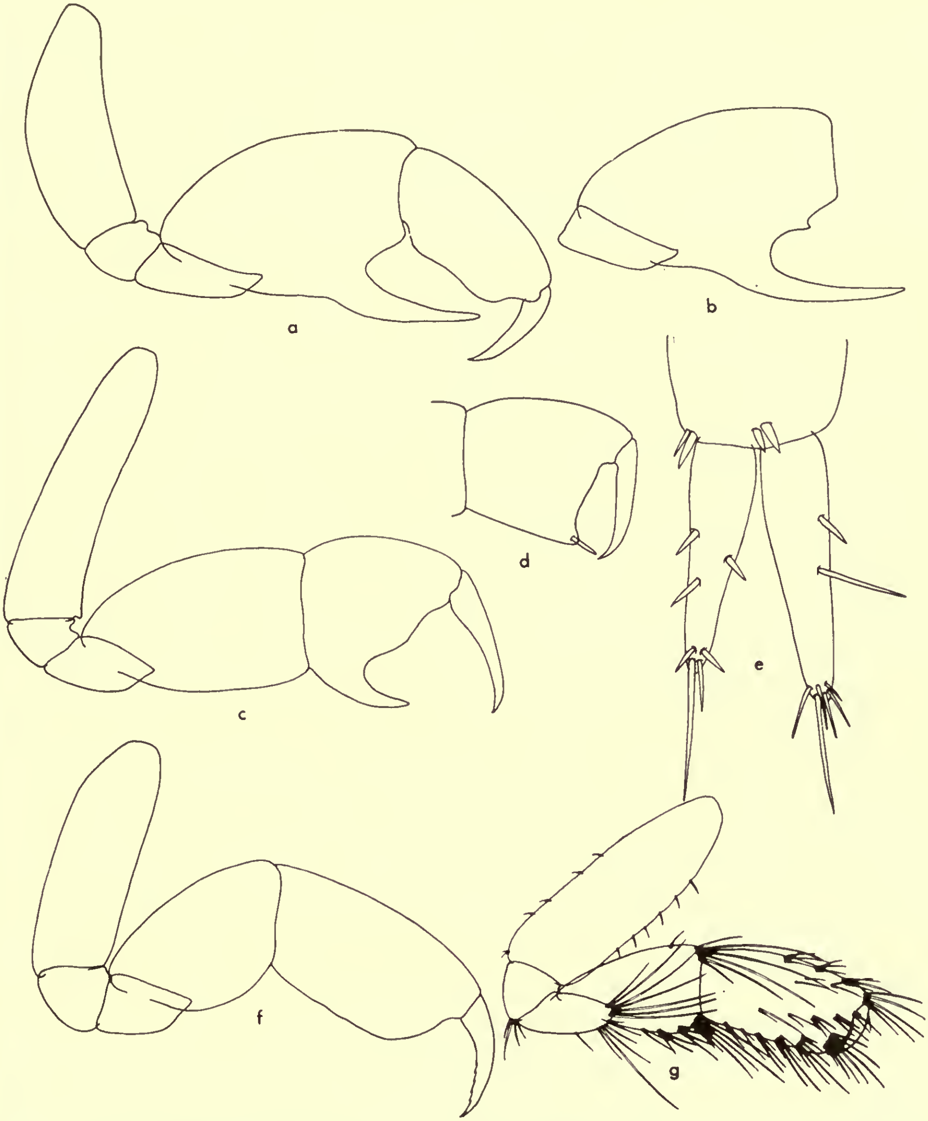

FIG. 19. *Microdeutopus chelifer* (Bate). (a) Male gnathopod 1, Paignton, Devon, England. (b) Male gnathopod 1, articles 4 and 5, Khios, Greece. (c) Male gnathopod 2, Paignton, Devon, England. (d) Male (Immature) gnathopod 2, articles 6 and 7, Khios, Greece. (e) Male uropod 3, Brittany, France. (f) Female gnathopod 1, Guernsey, Channel Islands. (g) Female gnathopod 2, Guernsey, Channel Islands.

Peraeon segments 2–4 each with an anteriorly directed process in the mid-ventral line, those of segments 2 and 3 long, slender, spiniform, that of segment 4 short, robust. *Gnathopod* 1 with article 1 strongly produced anteriorly, very acute; article 2 scarcely expanded; article 5 very enlarged, but longer than broad, the posterior margin produced sub-distally into a long, narrow, inward curving tooth, distal to which in some, but not all specimens, is a further small tooth; article 6 relatively long, the posterior margin undulate; article 7 robust. *Gnathopod* 2 with article 2 narrow and elongate, with a small projection at the antero-distal corner; article 6 shorter and broader than article 5, with the palmar region produced into a process, which in young males is short and broad, bearing a stout spine at its tip, but in mature males is drawn out into a long inward curving tooth, when the spine is usually obsolete; article 7 very long, opposable to the palmar process. *Uropod* 3 with the rami elongate and slender, subequal in length with the peduncle;

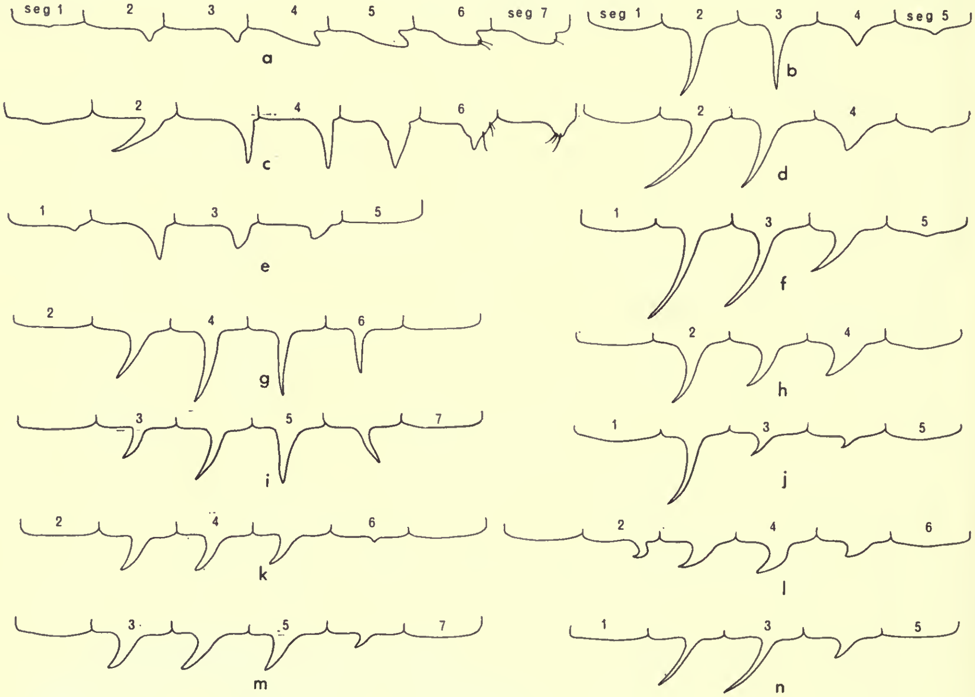

FIG. 20. Ventral peraeon processes in *Microdeutopus* species. (a) *M. gryllotalpa* Costa Isefjord, Denmark. (b) *M. anomalus* (Rathke) Falmouth, Cornwall, England. (c) *M. versiculatus* (Bate) Falmouth, Cornwall, England. (d) *M. anomalus* (Rathke) Plymouth, Devon, England. (e) *M. stationis* Della Valle Guernsey, Channel Islands. (f) *M. algicola* Della Valle Bône, Algeria. (g) *M. trichopus* Myers Isabela Island, Galapagos. (h) *M. damnoniensis* (Bate) Bandol, France. (i) *M. sp. nov.* ? Tortugas, Florida, U.S.A. (j) *M. damnoniensis* (Bate) Plymouth, Devon, England. (k) *M. hancocki* Myers Bahia de Salinas, Costa Rica. (l) *M. armatus* Chevreux Villefranche, France. (m) *M. schmitti* Shoemaker Bahia de Salinas, Costa Rica. (n) *M. chelifer* (Bate) Jersey, Channel Islands.

exopodite slightly the longer of the two rami, with two isolated spines on the outer margin, of which the more distal is particularly long; endopodite with two well separated spines on the inner margin and one on the outer; each ramus with a terminal cluster of spines, of which one is greatly elongated. *Telson* with each terminal crest bearing on its distal dorsal margin, a group of up to 3 setae.

Maximum size of male : 8 mm.

FEMALE. As the male except for the absence of ventral peraeon spines and the sexually dimorphic *antennae* and gnathopoda. *Antenna* with the third peduncular article unmodified, and the entire appendage less well developed than that of the male, such that it does not exceed the length of the antennule. *Gnathopod* 1 with article 2 moderately expanded; article 6 longer than article 5, about twice as long as broad, with the anterior and posterior margins roughly parallel; article 7 robust, equal in length to the palmar region. *Gnathopod* 2 similar to gnathopod 1 but more slender, the palmar region more transverse.

Maximum size of female : 8 mm.

DISCUSSION. As in the preceding species, the second gnathopoda of the male are chelate. In the present species, however, article 6 of this appendage (Text-fig. 19c) is much shorter and broader than article 5, whereas in *M. armatus* (Text-fig. 18d) the fifth and sixth articles are more or less subequal in length and breadth. *M. chelifer* is unique among the known *Microdeutopus* species in having sexually dimorphic antennae, but this feature is not considered to be a sufficient reason for separating the present species from the genus *Microdeutopus* (see also Stebbing, 1888). Females have few diagnostic characters, but important identification features when taken in combination are: the accessory flagellum of the antennule having three articles (Text-fig. 17a), the third uropod rami having their sparse spination of *solitary* spines, the more distal of two spines on the outer margin of the exopodite being exceptionally long (Text-fig. 19c) and the telson bearing setae, but no spines.

ECOLOGY. In the scarcely tidal Mediterranean the present species occurs in shallow waters, among *Cystoseira*, *Chondrus*, *Saccorhiza* etc. On the Atlantic and English Channel coasts, the species is also found in the shallow sub-littoral among *Laminaria* holdfasts and other weeds, but it most frequently inhabits the littoral zone, among algae in rock pools often high up on the shore, particularly in sheltered places with a high accumulation of silt, often where there is some brackish water influence.

DISTRIBUTION. Along the south-western coasts of the British Isles (Studland, Torbay, Wembury Bay, Salcombe, Portwrinkle), the Channel Islands and the adjoining French coast, and thence at a number of localities along the coasts of the Bay of Biscay to Guethery in the extreme south. Recorded from Cadiz, and probably occurs in a number of favourable localities around the coasts of Spain and Portugal. In the Mediterranean it has been recorded from the coast of France (Sète, Monaco, Antibes, Villefranche) and in the Aegean from the Greek Island of Khios, off the Turkish coast. The ?*Stimpsonia* sp. of Sowinsky (1898) from the Black sea may refer to this species.

Microdeutopus sporadhi sp. nov.

(Text-figs. 21, 22)

DESCRIPTION OF MALE HOLOTYPE. *Mouthparts* not differing significantly from those of other members of the genus. *Head* lateral-lobes moderately well developed, obtuse; eye reniform. *Antennule* about two thirds the body length, the first peduncular article shorter than the second, the third less than one half the length of the second; flagellum about one and one half the length of the peduncle, with thirteen articles; accessory flagellum with two articles, the second article minute, shorter than the first article of the primary flagellum. *Antenna* shorter than the antennule, the fourth and fifth peduncular articles subequal; flagellum scarcely longer than the fifth peduncular article, with seven articles. *Peraeon* segments 2 and 3 each with a robust, anteriorly directed spine in the mid-ventral line, that of segment 2 the longer. *Gnathopod* 1 with article 1 strongly produced anteriorly, somewhat attenuated, article 2 elongate, relatively slender, but broadening distally, its anterior margin excavate for the reception of the carpus when folded, article 4 slender, scarcely over lapping the posterior margin of article 5, article 5 grossly expanded, longer than broad,

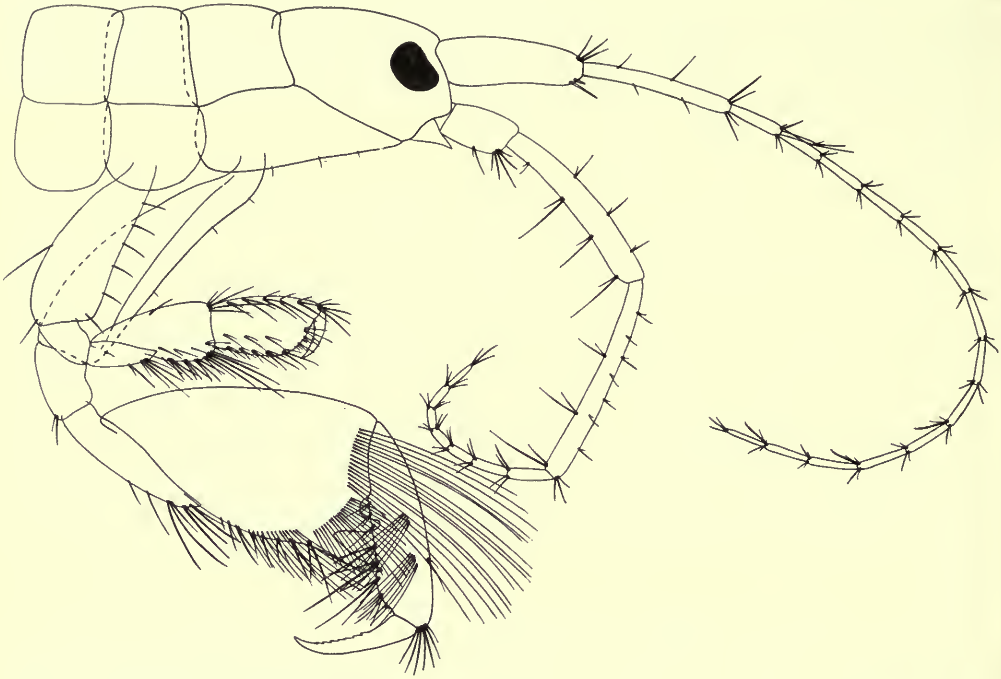

FIG. 21. *Microdeutopus sporadhi* sp. nov. Anterior end of male holotype, Emborios Bay, Khios, Greece.

slender basally, broad distally, with groups of long fine setae arising from within the distal and postero-distal margins, and with the posterior distal angle produced into two distinct teeth, the proximal (outer) tooth curved inward, relatively long and slender, terminating acutely, the distal (inner) short, robust, obtuse, article 6 elongate and slender, broadening somewhat distally, but with the palmar region almost obsolete, the posterior margin almost straight, article 7 very long, though slightly shorter than article 6, with accessory teeth on the posterior margin. *Gnathopod* 2 with article 2 relatively short and broad, the anterior margin almost straight, articles 5 and 6 subequal in length and breadth, article 7 relatively short. *Peraeopods* 3–7 of the typical *Microdeutopus* structure. *Uropod* 3 with the rami short, not exceeding the length of the peduncle, exopodite slightly the longer of the two rami, devoid of spines on the lateral margins, terminating distally in a group of five long setae, of which the two most distal arise from a vestigial second article; endopodite with a single median spine on the inner margin and a group of four

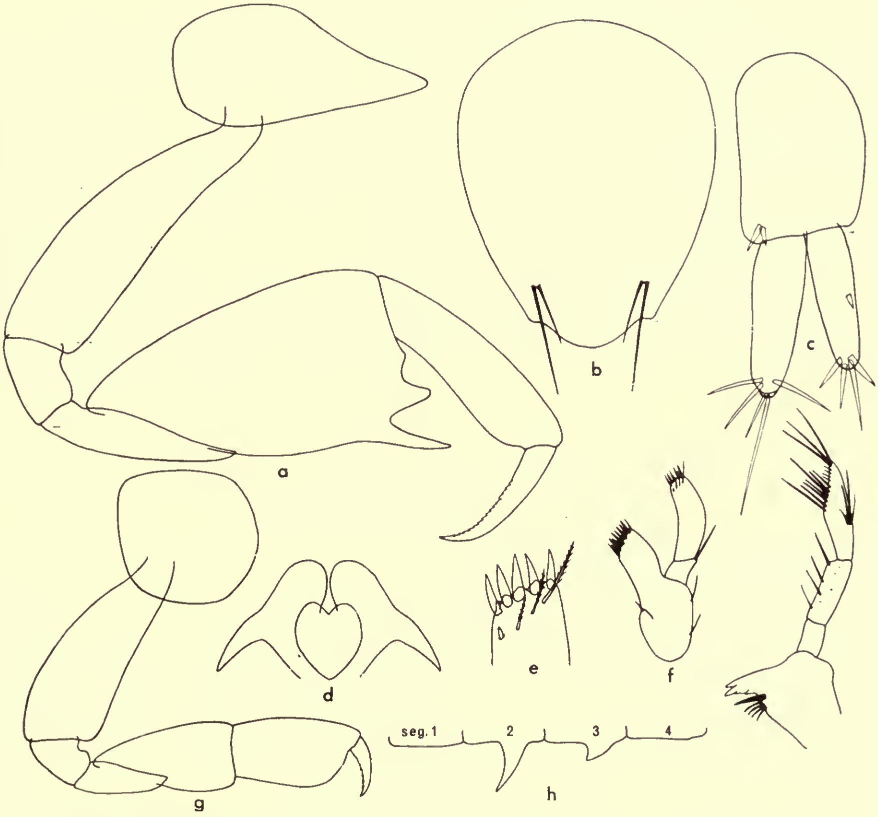

FIG. 22. *Microdeutopus* sporadhi sp. nov. Male paratypes. (a) Gnathopod 1. (b) Telson. (c) Uropod 3. (d) Paragnath. (e) Terminal article of maxillule palp. (f) Maxillule. (g) Gnathopod 2. (h) Ventral peraeon processes. (i) Mandible.

terminal setae. *Telson* of the usual *Microdeutopus* form, each terminal crest bearing on its distal dorsal margin a pair of long setae of unequal length.

Length : 3·0 mm.

MALE PARATYPES. Agree closely with the holotype in all diagnostic characters. Antennal flagellum of one paratype with 8 articles, otherwise this appendage also invariable.

Length of paratypes 2·8–3·2 mm.

FEMALE. Unknown.

TYPES. ♂ Holotype B.M. (N.H.) Registration Number 1968.1.8.1
1 ♂ Paratype B.M.(N.H.) Registration Number 1968.1.8.2
2 ♂ Paratypes U.S.N.M. Catalogue number 122544.

TYPE LOCALITY. Emborios Bay, Khios, Greece.

MATERIAL. 6 ♂ from the type locality, August 8–11th, 1967.

DISCUSSION. *M. sporadhi* does not show close affinity with any of the previously described species of *Microdeutopus*. Males differ from those of all other *Microdeutopus* species except *M. haswelli* Stebbing in the structure of gnathopod 1 (Text-fig. 22a), which has the posterior distal angle of article 5 produced into two teeth, of which the proximal (outer) is the longer. They differ from *M. haswelli* in the structure of the antenna (Text-fig. 21), which is slender, with a relatively elongate and slender flagellum, whereas in *M. haswelli* (Text-fig. 4b) it is sub-pediform, with the first flagellar article stout and the terminal articles compressed and obscurely articulate. In addition article 2 of gnathopod 2 is broad and relatively short in *M. sporadhi* (Text-fig. 22g), but elongate and very slender in *M. haswelli* (Text-fig. 3h).

ECOLOGY. Type material from among *Cystoseira* in 0–2 metres where relatively little water movement has allowed accumulation of detritus. Absent from *Cystoseira* growing nearby in deeper waters where there is relatively little detritus accumulation.

INCERTAE SEDIS

Genus ***Hansenella*** Chevreux 1909

Hansenella longicornis Chevreux, 1909 : 5, fig. 3.

The genus *Hansenella* was established by Chevreux (1909) for the reception of three ovigerous females obtained off the Azores at a depth of 1360 metres. The genus is characterized by the form of the female gnathopod 1, which is similar to that of male *Microdeutopus* species. In the light of the present review, this feature alone is not sufficient to erect a new genus, since development of teeth on article 5 of the female gnathopod 1 also occurs in *M. schmitti* Shoe. When males of *H. longicornis* are known, it is likely that the species will have to be transferred to the genus *Microdeutopus*, but it should be emphasized that the female gnathopod 1 is far more massively developed in *H. longicornis* than in any known *Microdeutopus* female.

SPECIES DUBIA

Microdeutopus tittii Heller

Microdeutopus tittii Heller, 1866 : 48, pl. 4, fig. 8.

It is doubtful if this form described from a single specimen collected at Pirano in the Adriatic is a distinct species. Della Valle (1893) considered it to be a much mutilated specimen of *M. gryllotalpa* Costa, but even allowing for mutilation, the undilated article 2 of gnathopod 2 would appear to precluds that species The relative lengths of the antennules and antennae could apply to *M. chelifer* (Bate), but the non-cheliferous gnathopod 2 precludes that species. Allowing for the mutilation of the antennules and antennae, which is of frequent occurrence in the delicate Aoridae, this species is most likely to be *M. anomalus* (Rathke) as suggested by Stebbing (1906) or *M. stationis* Della Valle. The long slender antenna with a flagellum of eleven articles would most favour the latter species.

Species not attributable to ***Microdeutopus*** Costa

1. *Microdeutopus anomalus* Bate, 1862 : 164. = ♀ *Aora typica* Kroyer, 1845 : 328.
2. *Microdeutopus arcticus* Hansen, 1887 : 231. = *Lembos arcticus* (Hansen) Stebbing, 1895 : 207.
3. *Microdeuteropus australis* Haswell, 1879 : 271 = *Lemboides australis* (Haswell) Stebbing, 1899 : 350.
4. *Microdeuteropus bidentatus* Stebbing, 1876 : 73. = *Lembos websterii* Bate, 1856 : 58.
5. *Microdeutopus kraemmeri* Reid, 1951 : 251. = *Lembopsis kraemmeri* (Reid) Myers, 1968c : In press.
6. *Microdeutopus longipes* (Lilljeborg) Bate, 1862 : 166. = *Lembos longipes* (Lilljeborg) Stebbing, 1895 : 207.
7. *Microdeutopus maculatus* Thomson, 1879 : 331. = ♀ *Aora typica* Kroyer, 1845 328.
8. *Microdeutopus megnae* Giles, 1888 : 231. = *Grandidierella megnae* (Giles) Chilton, 1921 : 548.
9. *Microdeuteropus mortoni* Haswell, 1879 : 339 = ♂*Aora typica* Kroyer, 1845 : 328.
10. *Microdeuteropus tenuipes* Haswell, 1879 : 339 = ♀*Aora typica* Kroyer, 1845 : 328.
11. *Microdeutopus tenuis* (Dana) Bate, 1862 : 165. = *Lembos tenuis* (Dana) Stebbing, 1895 : 207.
12. *Microdeutopus tridens* Schellenberg, 1938 : 74 = *Lembopsis tridens* (Schellenberg) Myers, 1968c : In press.
13. *Microdeutopus websterii* (Bate, 1862) : 164. = *Lembos websterii* Bate, 1856 : 58.

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APPENDIX I

Catalogue of material examined in the present work.

KEY TO ABBREVIATION OF SOURCES:

A.A.M.	Personal collections
A.M.S.	Australian Museum Sydney
B.M.N.H.	British Museum (Natural History)
E.R.	Dr. E. Rasmussen
M.B.A.P.	Marine Biological Association, Plymouth
M.N.H.N.	Museum National D'Histoire Naturelle, Paris.
S.B.A.	Station Biologique D'Arcachon
U.S.C.	University of Southern California
U.S.N.M.	United States National Museum (Smithsonian Institution)
U.Z.M.D.	Universitets Zoologiske Museum, Denmark.

* Indicates material emanating from the collections of the original author of the species.

	Location	No. of samples	Material
Microdeutopus gryllotalpa Costa			
England			
Chaldon Herring, Dorset	U.Z.M.D.	1	7 ♂ 18 ♀
Weymouth, Dorset	B.M.N.H.	1	1 ♂ 2 ♀
Plymouth, Devon	B.M.N.H.	1	1 ♂ 1 ♀ 3 immature
Wales			
Swansea, Glamorgan	A.A.M.	—	500 ♂ 500 ♀ 1000 immature
Denmark			
" Denmark "	B.M.N.H.	1	2 ♂ 2 ♀
Bohuslen	U.Z.M.D.	1	2 ♂
Isefjord	E.R.	18	43 ♂ 56 ♀ 13 immature
Roskilderjord	E.R.	3	3 ♂ 4 ♀
France			
Le Croisic	B.M.N.H.	1	3 ♂ 3 ♀
Arcachon	S.B.A.	1	31 ♂ 21 ♀
Spain			
Valencia	B.M.N.H.	1	3 ♀
Italy			
Naples	B.M.N.H.	2	5 ♂ 9 ♀
Greece			
Khios	A.A.M.	—	17 ♂ 26 ♀
U.S.A.			
" N.E. America "	B.M.N.H.	1	1 ♂ 1 ♀
Wood's Hole, Mass.	U.S.N.M.	7	20 ♂ 37 ♀
Marion Harbour, Mass	U.S.N.M.	1	2 ♀
Vinyard Sound, Mass.	U.S.N.M.	7	72 ♂ 102 ♀ 4 immature
Newport, Rhode Island	U.S.N.M.	4	4 ♂ 3 ♀ 1 immature
Noank, Connecticut	U.S.N.M.	4	8 ♂ 13 ♀ 8 immature
Microdeutopus versiculatus (Bate)			
England			
Plymouth, Devon	A.A.M.	—	4 ♂ 11 ♀
	B.M.N.H.	2	3 ♂ 7 ♀
	U.Z.M.D.	1	1 ♂ 1 ♀
	M.B.A.P.	1	1 ♂ 1 ♀
Salcombe, Devon	B.M.N.H.	1	1 ♀
Mouth of river Yealm, Devon	B.M.N.H.	1	5 ♂ 10 ♀ 2 immature
Falmouth, Cornwall	B.M.N.H.	2	21 ♂ 19 ♀ 4 immature
	U.Z.M.D.	1	7 ♂ 6 ♀
Scotland			
Isle of Mull	B.M.N.H.	3	3 ♂ 6 ♀
Oldany Harbour, Sutherland	U.Z.M.D.	1	3 ♀
Eire			
Birterbuy Bay, Co. Galway	B.M.N.H.	2	4 ♂ 8 ♀ 2 immature
Roundstone, Co. Galway	B.M.N.H.	1	9 ♂ 12 ♀ 2 immature
Westport, Co. Mayo	B.M.N.H.	1	3 ♂ 8 ♀
Channel Islands			
Guernsey	B.M.N.H.	1	9 ♂ 15 ♀
Microdeutopus stationis Della Valle			
Channel Islands			
St. Peter's Port, Guernsey	B.M.N.H.	1	14 ♂ 6 ♀

	Location	No. of samples	Material
Corsica			
Bonifacio	M.N.H.N.	1	1 ♀
Italy			
*Naples	B.M.N.H.	2	4 ♂ 11 ♀ 1 immature
Algeria			
Bône	M.N.H.N.	1	1 ♂ 2 ♀
Greece			
Khios	A.A.M.	—	3 ♂ 1 ♀
Microdeutopus haswelli Stebbing			
Australia			
Port Jackson	A.M.S.	1	1 ♂ HOLOTYPE
Microdeutopus anomalus (Rathke)			
England			
Plymouth, Devon	A.A.M.	—	127 ♂ 264 ♀ 149 immature
Falmouth, Cornwall	B.M.N.H.	1	64 ♂ 67 ♀ 21 immature
	U.Z.M.D.	1	1 ♂
Scotland			
Argyll	B.M.N.H.	2	5 ♂ 5 ♀
Isle of Mull	B.M.N.H.	2	13 ♂ 61 ♀
Eire			
Birterbuy Bay, Co. Galway	B.M.N.H.	1	40 ♂ 50 ♀ 45 immature
Westport, Co. Mayo	B.M.N.H.	1	1 ♂ 1 ♀
Valentia, Co. Kerry	B.M.N.H.	1	4 ♂ 5 ♀ 1 immature
Killiebegs, Co. Donegal	B.M.N.H.	1	1 ♂ 9 ♀ 3 immature
Norway			
" Norway "	B.M.N.H.	1	1 ♀
Denmark			
Bohuslen	B.M.N.H.	1	1 ♂ 1 ♀
	U.Z.M.D.	1	1 ♂ 1 ♀
France			
Cette	M.N.H.N.	1	2 ♂
Corsica			
Bonifacio	M.N.H.N.	1	7 ♂ 26 ♀ 12 immature
U.S.A.			
Wood's Hole, Mass.	U.S.N.M.	4	11 ♂ 17 ♀
Marion Harbour, Mass.	U.S.N.M.	1	2 ♀
Vinyard Sound, Mass.	U.S.N.M.	8	15 ♂ 18 ♀
Rivers' Island, Mass.	U.S.N.M.	1	2 ♀
Provincetown, Cape Cod. Mass.	U.S.N.M.	1	2 ♂ 3 ♀
Newport, Rhode Island	U.S.N.M.	4	5 ♂ 23 ♀ 2 immature
No Data	U.S.N.M.	1	1 ♀
Microdeutopus damnoniensis (Bate)			
England			
Plymouth, Devon	B.M.N.H.	1	1 ♂ LECTOTYPE 4 ♀ PARALECTOTYPES
Wembury, Plymouth, Devon.	B.M.N.H.	1	2 ♀ 2 immature
Drake's Island, Plymouth Devon	U.Z.M.D.	1	8 ♂ 7 ♀ 3 immature

	Location	No. of Samples	Material
Channel Islands			
Jersey	B.M.N.H.	1	2 ♂ 4 ♀
Guernsey	B.M.N.H.	1	2 ♀
France			
Bandol	M.N.H.N.	1	6 ♂ 10 ♀ 2 immature
Microdeutopus algicola Della Valle			
Italy			
*Naples	B.M.N.H.	1	1 ♂ 1 ♀
Algeria			
Bône	M.N.H.N.	1	1 ♂
Microdeutopus schmitti Shoemaker			
U.S.A.			
Point Conception, California	U.S.C.	2	24 ♂ 64 ♀ 24 immature
Point Loma, California	U.S.C.	2	5 ♂ 5 ♀ 2 immature
San Clemente, California	U.S.C.	1	3 ♂ 2 ♀
Newport, California	U.S.C.	6	3 ♂ 6 ♀ 1 immature
Mexico			
El Coyote, Baja California	U.S.N.M.	1	1 ♂
Bahia de San Quintin, Baja, California	U.S.N.M.	1	7 ♂ 19 ♀
Bahia de Magdalena Baja California	U.S.C.	1	2 ♀
Costa Rica			
Bahia de Salinas	U.S.N.M.	9	514 ♂ 261 ♀ 50 immature
Playa Blanca	U.S.N.M.	2	3 ♂
South Viradores Islands	U.S.N.M.	1	1 ♂
Microdeutopus hancocki Myers			
Costa Rica			
Bahia de Salinas	U.S.N.M.	2	21 ♂ TYPE MATERIAL
Panama			
Bahia Honda	U.S.N.M.	2	12 ♂ 23 ♀ 4 immature
Equador			
Salango Island	U.S.N.M.	1	1 ♂
Galapagos			
Isabela Island	U.S.N.M.	1	21 ♂ 23 ♀ 4 immature
Microdeutopus trichopus Myers			
Galapagos			
Isabela Island	U.S.N.M.	3	38 ♂ 3 ♀ TYPE MATERIAL
Microdeutopus sp. nov?			
U.S.A.			
Tortugas, Florida	U.S.N.M.	2	2 ♂ 1 ♀
Microdeutopus armatus Chevreux			
France			
* Le Croisic	B.M.N.H.	1	3 ♂ 3 ♀
* Antibes	M.N.H.N.	1	2 ♂ 8 ♀
* Villefranche	M.N.H.N.	1	13 ♂ 17 ♀

	Location	No. of samples	Material
Microdeutopus chelifer (Bate)			
England			
Salcombe, Devon	B.M.N.H.	1	1 ♂ HOLOTYPE
Wembury Bay, Plymouth, Devon	U.Z.M.D.	1	3 ♂ 1 ♀
Paignton and Torbay, Devon	B.M.N.H.	1	2 ♂ 1 ♀
Studland, Dorset	U.Z.M.D.	1	1 ♂
Channel Islands			
Guernsey	B.M.N.H.	1	1 ♂ 1 ♀
Jersey	U.Z.M.D.	1	1 ♂ 1 ♀
France			
Brittany	B.M.N.H.	1	3 ♀
Le Croisic	B.M.N.H.	1	3 ♀
Greece			
Khios	A.A.M.	—	39 ♂ 43 ♀
Microdeutopus sporadhi sp. nov.			
Greece			
Khios	A.A.M.	—	6 ♂

APPENDIX II

Location of type material of *Microdeutopus* species

M. haswelli Stebbing	Holotype	A.M.S. 3497
M. damnoniensis (Bate)	Lectotype	B.M.N.H. 1967.11.1.1
	Paralectotypes	B.M.N.H. 1967.11.1.2–5
M. schmitti Shoemaker	Holotype	U.S.N.M. 79375
M. hancocki Myers	Holotype	U.S.N.M. 112797
	Paratypes	U.S.N.M. 112798–9
		B.M.N.H. 1967.7.2.1–4
M. trichopus Myers	Holotype	U.S.N.M. 112800
	Paratypes	U.S.N.M. 112801–2
		B.M.N.H. 1967.7.2.5–6
M. chelifer (Bate)	Holotype	B.M.N.H. 1952.5.7.129
M. sporadhi sp. nov.	Holotype	B.M.N.H. 1968.1.8.1
	Paratypes	B.M.N.H. 1968.1.8.2
		U.S.N.M. 122544

Type material of *M. versiculatus* (Bate) is not present in Bate's collections at the British Museum (Natural History) and is therefore probably non-existant. Type material of species described by Costa, Della Valle, Rathke and Chevreux has been untraceable.

PLATE 1

Microdeutopus hancocki Myers
(a) Male paragnaths, Bahia de Salinas, Costa Rics.
Microdeutopus schmitti Shoemaker
(b) Male paragnaths, Bahia de Salinas, Costa Rica.

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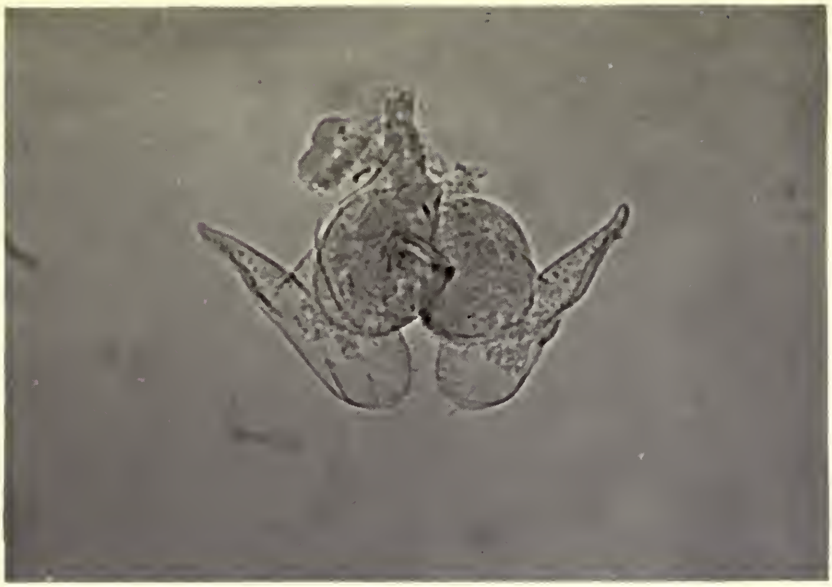

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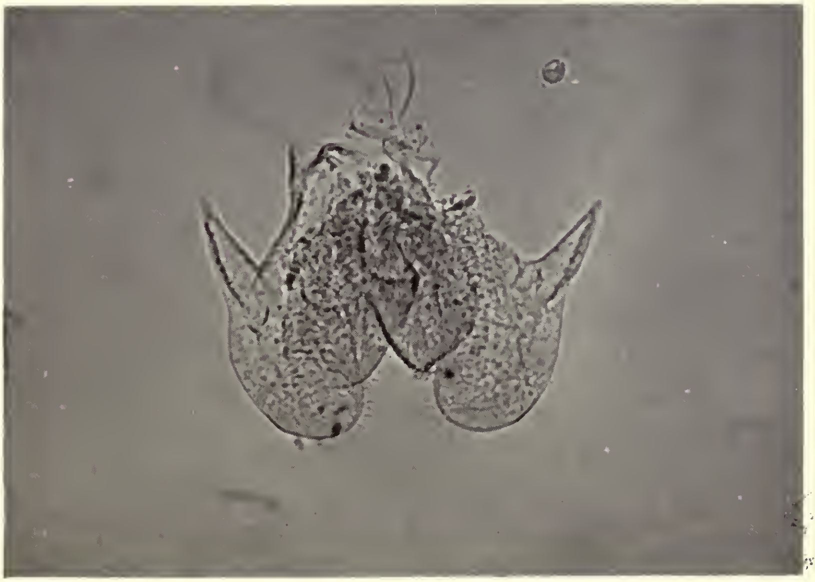

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CONVERGENCE IN THE STRUCTURE OF THE HEAD AND CUTICLE OF *EUCHROMADORA* SPECIES AND APPARENTLY SIMILAR NEMATODES

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TRUSTEES OF
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CONVERGENCE IN THE STRUCTURE OF THE HEAD AND CUTICLE OF *EUCHROMADORA* SPECIES AND APPARENTLY SIMILAR NEMATODES

By W. GRANT INGLIS

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SYNOPSIS

The comparative anatomy and structure of the head and cuticle is described in several species of *Euchromadora* and a number of other morphologically very similar species in which the cuticle is complex and heterogeneous and the lateral pieces of the gubernaculum are massive and typically L-shaped. *Euchromadora* species are characterized by a solid dorsal onchium, a series of denticles in transverse rows on both the lateral and ventral walls of the oesophastome, a cuticle in which the large punctations are due to the presence of processes arising from one side of each cuticular annule and there are no markings on the cuticle along the dorsal and ventral surfaces over much of the length of the body. Other *Euchromadora*-like species which in the past have been described as having an anteriorly directed dorsal onchium are shown to possess hollow-type dorsal onchia; flanges on the lateral walls of the oesophastome; anteriorly directed, cone-like onchia on the ventral sectors of the oesophastome; a cuticle in which the large punctations are frequently due to processes developed from both sides of each cuticular annule and there are markings on the cuticle of the dorsal and ventral surfaces along the whole length of the body. As a result the following major taxonomic changes are proposed. *Euchromadora* de Man, 1866 retains seven species: *E. vulgaris* (Bastian, 1865), type species of the genus; *E. gaulica* Inglis, 1962; *E. meadi* Wieser & Hopper, 1967; *E. permutabilis* Wieser, 1954; *E. striata* (Eberth, 1863); *E. tokiokai* Wieser, 1955; *E. eileenae* sp. nov. *STEINERIDORA* Gen. Nov. is very similar to *Euchromadora* but has large, sickle-like onchia arising from both the lateral and ventral walls of the oesophastome and a distinct posterior oesophageal bulb. It contains the following four species: *S. loricata* (Steiner, 1916), type species of the genus; *S. adriatica* (von Daday, 1901); *S. archaica* (Steiner & Hoeppli, 1926); *S.* (?) *dubia* (Steiner, 1918) *species inquirenda*. In the remaining genera the dorsal onchium is hollow. *Graphonema* Cobb, 1898 is rediagnosed on the basis of Australian specimens which are undoubtedly congeneric with those described by Cobb so that this genus is characterized by a swollen, set-off head, and two circles of cephalic setae. It contains the following species: *G. vulgaris* Cobb, 1898, type species of the genus; *G. georgei* sp. nov.; *G. amokurae* (Ditlevsen, 1921) Wieser, 1954. The rediagnosis of *Graphonema* displaces species in which the dorsal onchium, although hollow, is controlled by a massive development of the dorsal oesophageal musculature, there is a posterior oesophageal bulb and the gubernaculum is small and not L-shaped. The four species involved are referred to a new genus *Innocuonema*: *I. flaccida* (Wieser, 1959) type species of the genus; *I. clovosa* (Wieser, 1959); *I. tentabunda* (de Man, 1890); *I. chilensis nom. nov. pro G. amokuroides* of Wieser, 1954. The discovery of *Nygmatonchus alii* Murphy, 1965 led to a reassessment of *Nygmatonchus* Cobb in Cobb, 1933 which is considered to contain four species: *N. scriptus* Cobb in Cobb, 1933, type species of the genus; *N. fossiferus* Wieser, 1954; *N. minutus* Gerlach, 1967; *N. bicornata* (Wieser, 1959) comb. nov., in all of which the cuticle is laterally differentiated, the amphid has a prominent double contour and there is a (?) pre-cloacal modification on the male body. *N. alii* is referred to a new genus *Austranema* with three other species: *A. colesi* (Inglis, 1968), type species of the genus; *A. alii* (Murphy, 1965); *A. pectinata* (Weiser & Hopper, 1967); *A. shirleyae* (Coles, 1965), characterized by the possession of a circle of ten cephalic setae, a head which is not set-off and the presence of a median pre-cloacal thickening on the ventral surface of the males. A new genus and species, *Parapinnanema wilsoni*, is described in which the cuticle is very thick and obviously battlement-like, the dorsal onchium is hollow and the lateral flanges of the oesophastome are not dentate anteriorly, the cephalic sense organs are in three circles of which the intermediate and outer are setae and there is a region of pre-cloacal modification on the males. Finally a new genus, *Protochromadora*, is proposed for three species: *P. scampae* (Coles, 1965), type species of the genus; *P. mediterranea* (Allgén, 1942); *P. parafricana* (Gerlach, 1958), in which there are no structures on the lateral walls of the oesophastome, the cuticle lacks punctations on the dorsal and ventral surface and there is no pre-cloacal modification on the ventral surface of the male. Five species are described from the coasts of Western Australia, thus: *Euchromadora striata* (Eberth, 1863); *E. eileenae* sp. nov.; *Graphonema georgei* sp. nov.; *Parapinnanema wilsoni* gen. et sp. nov.; and *Hypodontolaimus slacksmithi* sp. nov. The classification of the Chromadoridae is briefly discussed in view of the recognition that complex cuticle, structure of the dorsal onchium, form and distribution of cephalic sense organs and shape of lateral pieces of the gubernaculum are not covariant. Nomenclatural changes are listed on page 201.

INTRODUCTION

The classification of the nematode family Chromadoridae Filipjev, 1917 is largely based upon the appearance of the cuticle and its associated lateral differentiation, the shape of the amphids and the gross form of the dorsal onchium which occurs in the buccal cavity. Thus de Coninck (1965) recognizes three subfamilies within the family: Chromadorinae with a solid dorsal onchium and non-spiral amphids; Hypodontolaiminae de Coninck, 1965 with a hollow dorsal onchium and non-spiral amphids; and Ethmolaiminae Filipjev & Schuurmans Stekhoven, 1941 with a hollow dorsal onchium and spiral amphids. Within each of these subfamilies genera are distinguished very largely by the distribution and form of the cephalic sense organs, the appearance of the cuticle, the presence or absence of lateral differentiation and the dentition of the buccal cavity.

Using such criteria the genus *Euchromadora* de Man, 1886 is apparently easily recognized by a blunt head, a prominent solid dorsal onchium, a characteristically dark and complicated cuticle and a gubernaculum of a unique L-shape. Several authors have drawn attention to the possible value of the detailed structure of the cuticle as a source of taxonomic data within the genus (Steiner & Hoeppli, 1926; Inglis, 1962; Coles, 1965; Wieser & Hopper, 1967) but it has rarely been studied in detail in one species (Steiner & Hoeppli, 1926; Inglis, 1964; Watson, 1965) and never comparatively in a number of species.

The peculiar and characteristic shape of the gubernaculum has generally been well described and appears to supply " One of the most decisive features of this genus . . ." (Wieser, 1954, page 101). However it has never been shown that the characteristic gubernaculum is consistently associated with the elaborate cuticle and the large solid onchium. Some doubt about this assumed covariance is raised by Murphy's (1965) description of *Nygmatonchus alii* Murphy, 1965 in which an L-shaped *Euchromadora*-type gubernaculum is associated with a complex cuticle and a hollow dorsal onchium. It will be shown below that this doubt is well justified.

The difference between a hollow and a solid onchium is spectacular and obvious when the extremes of both conditions are compared but intermediate forms occur which I have found difficult, if not impossible, to classify in this way with accuracy. It was, therefore, thought necessary to establish whether the hollow and solid onchia are associated with other more easily distinguished features before accepting this difference as a basis for classification.

The difficulty of distinguishing between the solid and hollow condition has arisen with others in the past since both Wieser (1954) and de Coninck (1965) refer *Spilophorella* Filipjev, 1918 to the solid-onchia group while to me all the illustrations of species referred to that genus, and all the specimens I have studied, are best described as possessing hollow onchia.

Similar confusion has arisen in another way since both Wieser (*loc. cit.*) and de Coninck (*loc. cit.*) group *Odontocricus* Steiner, 1918 and *Dicriconema* Steiner & Hoeppli, 1926, in both of which the cuticle is complex, with those genera in which a solid dorsal onchium is definitely present. This can only have been based on an assumption of covariance between the solid onchium and the complex cuticle since in neither case is any information available about the structure of the dorsal onchium. In *Dicriconema* the illustration of the anterior end of the body given by Steiner & Hoeppli (1926, Pl. 1, fig. 1) suggests that the dorsal onchium is hollow while the uninformative description of *O. hupferi* Steiner, 1918 simply mentions the presence of a dorsal onchium. However this description is preceded by a description of *Euchromadora luederitzi* Steiner, 1918 in which the dorsal onchium is illustrated as hollow.

The unreliability of the gross appearance of the cuticle as an indicator of other similarities is understandable when we recall the functional importance in the Nematoda of a cuticle which is longitudinally flexible while tangentially strong (Inglis, 1964). Attention has already been drawn to the narrow morphological range within which the cuticle could be, or has been, modified (Inglis, 1965) so that it is easy to appreciate that massive convergence in the appearance of the cuticle is more likely to be the rule than the exception. Such convergences are unlikely to be recognized so long as the structure of the cuticle is considered under such simple headings as homogeneous/heterogeneous, simple/complex. However, the complexity of the cuticle in some forms leads to very great difficulties in analysing its structure in any greater detail than is implied by such simple groupings and here again it is necessary, if possible, to establish the co-occurrence of other more easily studied features.

It is clear that, as de Coninck (1965) stresses, the taxonomy of the Family Chromadoridae is in need of examination but it is difficult to see that any such revision can be based upon a reassessment of the kind of information generally available. Too much of the present classification is fortuitous, too many of the groupings recognized are based on bibliographical information and too many of the morphological studies have been carried out with the sole aim of delimiting species. The major difficulties in overcoming this are the time needed to carry out comparative studies and the small size of the specimens involved.

I have been able to carry out some such comparative studies on specimens collected from the coasts of Western Australia. The specimens are in some cases confusingly *Euchromadora*-like in appearance but detailed examination disclosed discrepancies which led me to study such species of the genus *Euchromadora* as were easily available in large numbers. The unexpected results are presented here.

MATERIALS AND METHODS

Almost all the specimens were killed and fixed by gathering seaweed by hand and putting it into plastic bags with seawater. Sufficient formalin was then added to the bags to make a 7% formalin solution. The bags were shaken and nematodes picked out later by hand under a stereoscopic dissecting microscope. Specimens were then studied under a compound microscope; uncleared and mounted in alcohol or cleared and mounted in glycerine (prepared by a slow method involving the evaporation of alcohol from an alcohol: glycerine mixture); or in lactophenol. The structure of the cuticle was examined in squashes, in whole mounts, by transmitted light, by phase contrast and after treatment with sodium hypochlorite. This latter method produces separate rings of the sclerotized annules and rods of the cuticle. Finally the rings of sclerotized cuticle were studied through crossed polaroid filters when their birefringence makes them stand out spectacularly.

The heads were studied by mounting in glycerine jelly in a few cases but, more commonly, they were mounted in liquid glycerine or lactophenol under cover-slips supported by lens cleaning tissue. This latter method allows the head to be tilted to any angle so that it can be studied in detail. In a few cases it was possible to evert the anterior end of the oesophagus through the mouth opening so that the dentition could be studied in great detail.

All whole mounts were fluid and temporary with the coverslips supported by paper so that it was possible to get a view of the animals from any angle by rolling.

The use of Cobb slides or other form of permanent mount is to be deprecated for morphological studies. Such slides are undoubtedly useful and simple for routine identification but are a grave handicap in establishing the taxonomy of any group of nematodes. The use of any permanent mount leads to the treatment of the animals being examined as two dimensional and to the description of plates, seen in optical section, as rods; to the description of flanges as teeth and to the analysis of solid curved structures as hollow or pierced by holes or channels.

Studies of the kind reported here are generally time consuming and sometimes difficult but experience in other fields of nematology has shown that *en face* views of the head, although not always essential in the delimitation of species, are essential in establishing any meaningful classification above the species level.

Most of the specimens studied were collected from various localities on the coast of Western Australia during October, 1966, but some were collected on the coasts of Europe, particularly the British Isles, and one sample originated from South Africa. The holotype males of all new species are deposited in the collections of the Western Australian Museum, Perth, Western Australia. Paratypes are deposited in the same institution and in the collections of the British Museum (Natural History), London, S.W.7.

Species Studied

Euchromadora adriatica (Von Daday, 1901)
Euchromadora colesi Inglis, 1968
Euchromadora eileenae sp. nov.
Euchromadora gaulica Inglis, 1962.
Euchromadora loricata (Steiner, 1916)
Euchromadora mediterranea Allgén, 1942.
Euchromadora scampae Coles, 1965.
Euchromadora shirleyae Coles, 1965.
Euchromadora striata (Eberth, 1863)
Euchromadora vulgaris (Bastian, 1865).
Graphonema georgei sp. nov.
Hypodontolaimus slacksmithi sp. nov.
Nygmatonchus alii Murphy, 1965
Parapinnanema wilsoni gen. et sp. nov.

THE STRUCTURE OF THE HEAD

The head of any nematode is derived developmentally from two sources, from the anterior end of the region of primary embryonic invagination, the stomodaeum, which becomes the oesophagus (there is some reasonable doubt about this interpretation of the oesophagus as a stomadaeum, which is generally overlooked, and the term is used here for convenience) and from a region of secondary overgrowth derived from the hypodermis. These two regions are generally easily distinguished in histological sections because the primary oesophageal region is lined by simple, structurally uniform cuticle while the secondary region is lined by cuticle which is continuous with and similar in appearance to the cuticle covering the outer surface of the body.

The entire mouth cavity of nematodes I have proposed should continue to be called the stoma; the region of secondary overgrowth continues to be known as the cheilostome while any region of specialization at the anterior end of the oesophagus (i.e. region of primary invagination) is the oesophastome (Inglis, 1965; 1967). The wall of the cheilostome is the cheilorhabdion and that of the oesophastome is the oesopharhabdion. Following Cobb's (1919) terminology as modified by Chitwood (1950) I use the term odontium for any tooth-like structure developed from the cheilostome and the term onchium for any similar structure developed from the oesophastome. For convenience the general term denticle will also be used in this paper to imply a small solid cuticular tooth-like structure developed from the oesopharhabdion.

The cheilostome in the Chromadoridae is typically shallow, without odontia but with a circular mouth opening surrounded by twelve rugae. In some cases the terminal processes of the rugae are lacking and there are twelve flange-like supporting structures which project into the cheilostome as curved wedges which may warrant description as odontia (see page 198).

The cuticle covering the anterior end of the body is either without punctations or, more posteriorly, the punctations are simple and rod-like. It is worth noting that when the cuticle in *Euchromadora* is stained with Mallory's Triple Stain this lightly punctate region stains various shades of light blue while the more elaborate punctate component posteriorly stains a dense orange-red. This difference in staining reaction appears to reflect a difference in the degree of sclerotization and flexibility of the cuticle, the blue regions being flexible while the orange-red are relatively rigid (Inglis, 1961).

In *Euchromadora* and similar forms, most of the variation in the structure and elaboration of the anterior end of the body is restricted to the oesophastome, into which a large dorsal onchium almost invariably projects. The oesophastome is in the form of a cup formed by an expansion of the lumen of the oesophagus at its anterior end. The cuticular walls of this oesophastomal cup are thick and prominent and form curved sheets which blanket the cup tangentially. The thickening of the cup extends posteriorly into the true tri-radiate lumen of the oesophagus where it becomes increasingly thin posteriorly until it ceases to be obvious (Text-figs. 3, 19, 43, 46).

The oesophastomal cup is roughly rectangular in transverse section (i.e. when viewed *en face*). The dorso-lateral radii of the oesophagus arise from the dorso-lateral corners of this rectangular cavity while the ventral arm of the lumen arises from the mid-point of the ventral side of the rectangle. The boundaries between the dorsal and lateral walls are, therefore, easily established by the dorso-lateral arms of the oesophageal lumen. The boundaries between the lateral and ventral walls (more correctly sub-walls for uniformity but called walls for convenience) are frequently set-off by somewhat similar ventro-lateral extensions of the lumen of the oesophagus. These extensions can be spectacularly obvious in some species. In all cases, however, the limits can be established not only by the shape of the oesophastome but also by the distribution of the modifications in the form of onchia and plates present on the lateral and ventral walls (Text-figs. 1, 6, 12, 13, 27, 30, 39, 42, 45, 47, 52, 58).

In typical *Euchromadora* species as exemplified by *E. vulgaris*, the type species of the genus, the dorsal wall of the oesophastome is fairly straight, in an *en face* view, and bears a series of wholly cuticular onchia (or denticles) along its anterior edge (Text-figs. 12, 13). Posterior to this level is the large, wholly cuticular onchium which projects into the oesophastome and articulates posteriorly on the thickened dorsal wall of the oesophastome.

The anterior, most dorsal, edge of the lateral walls projects inwards over the cavity of the oesophastome as a pointed, somewhat onchium-like flange which arises from the ventral edge of the dorso-lateral radii of the lumen of the oesophagus. Posterior to this extreme anterior edge the lateral walls bear a series of wholly cuticular, generally tiny, denticles which run roughly dorso-ventrally (i.e. transversely when viewed from the lateral aspect of the body) in distinct rows, of which four can usually be recognized. In some cases one or more of these onchia is larger than the others and the rows may be straight or bent (Text-figs. 2, 17, 24, 34).

The ventral walls of the oesophastome also bear a series of small, wholly cuticular denticles with, usually, a series of much more prominent solid onchia arising from a basal plate low down in the oesophastome or from the border between the ventral walls and the median-ventral extension of the lumen of the oesophagus (Text-figs. 1, 6, 12, 13, 25, 27 etc.).

In all the species in which the dorsal onchium is unequivocably hollow, and in many in which no decision can be easily reached, the conditions are consistently different. The oesophastome is still in the form of a rectangular cup with thickened cuticular walls but the dorsal onchium is not, or not obviously, solid. This means that the musculature controlling it passes into the lumen of the onchium and does not attach to its base as in solid onchia. The anterior edge of the oesophastomal cup, which is generally strongly curved dorsally, is not dentate along its anterior edge, while ventrally and laterally there are no rows of small denticles. Instead two large cone-like cuticular onchia arise from the ventral floor of the oesophastome with, in some species, another smaller similar pair which arises from the edge of the ventral lumen (Text-figs. 30, 39, 42, 45, 52).

The lateral walls of the oesophastome do not bear series of denticles, instead, there is a cuticular flange which stands independent of, but parallel to each lateral wall (Text-figs. 44, 45, 52, 54). The anterior edge of this flange is generally higher towards the dorsal surface of the body than the ventral and in some species is divided along its anterior edge to produce a series of tooth-like points which project wholly anteriorly. When viewed from the ventral aspect this flange looks like a tooth arising from the lateral wall of the oesophastomal cup (Text-fig. 54; see also Fig. 21 in Coles, 1965). Its shape in *en face* views is very characteristic because it stands free more posteriorly on its ventral edge than it does on its dorsal. This means that when viewed in optical section *en face* it gives the appearance of being a ventrally curved hook-like derivative from the wall of the oesophastome. The shape of this lateral flange and the presence and distribution of the ventral cone-like onchia is shown by Murphy (1965) in his figure of the head of *Nygmatonchus alii* (Murphy's Fig. 1, D).

In all species the head bears sixteen cephalic sense organs of which six are arranged in a circle near the edge of the mouth opening while the remainder may be arranged in one circle of ten or as an intermediate circle of six and an outer circle of four. In all the definitely *Euchromadora* species usually the outer sense organs only are in the form of setae while in the others the intermediate circle is also composed of setae.

THE STRUCTURE OF THE CUTICLE

The structure of the cuticle will be considered in detail later but it is only fair to stress at this point that its analysis is very difficult. However the following features are common to all those species with complex cuticles. The cuticle, except the extreme anterior end, is dark in colour, thick and marked by large, elongate punctations anteriorly, at least. In addition, in many forms, the components of the cuticle appear to move when the focus is adjusted under very high magnifications. This elaborate structure is best understood against the functional background imposed by the design of the nematode body but I would point out that I have never been able to find any indication of fine " lines " connecting the punctations in a network or any other arrangement.

The long, thin cylindrical nematode body with its system of longitudinal muscles operating against an internal hydrostatic pressure produces two inevitable and conflicting mechanical requirements: longitudinal flexibility combined with radial or tangential strength (Inglis, 1964). This has been overcome during the evolution of various groups of nematodes in one of, or a combination of both of, two ways: by the evolution of either a system of cross spiral, helically arranged fibres or a series of transverse rings of dense material within the cuticle.

The spiral fibre method resolves both problems at the same time but the transverse ring method introduces further problems, particularly a loss of flexibility and the presence of regions of relative weakness in the cuticle between the strong, dense rings of sclerotized material. The latter problem has been resolved in a number of ways such as the development of overlapping flaps of dense material which lie over the weaker, less dense inter-annular material or by the development of tiling (de Coninck, 1942). The most complicated method, however, appears to be that evolved in some of the Chromadoridae, particularly those referred to the genus *Euchromadora*, in which the inter-annular regions are strengthened by processes bridging the gaps between the annules like the teeth of a comb.

In the typical *Euchromadora* species, in which the dorsal onchium is massive and solid and the oesopharhabdion bears series of small denticles, the cuticle always has non-punctate regions running down the dorsal and ventral surfaces of the body (see Coles, 1965, Fig. 1 and discussion) while in the hollow onchium forms, in which there are flanges laterally in the oesophastome, the cuticle does not have clear strips dorsally and ventrally. Instead elongate punctations occur over the whole surface of the body along its whole length, except on four regions, dorso- and ventro-lateral in position, where the punctations are replaced by prominent articulating plates (see Text-fig. 68 and also Steiner & Hoeppli, 1926, Pl. 1, 2, figs. 1, 3, 4, 5).

The non-punctate region of the cuticle at the anterior end of the body is shallow and, as a corollary, the amphids tend to lie near the anterior end in *Euchromadora* species, while in the other group of species this non-punctate region is relatively extensive and the amphids lie relatively far posteriorly. The amphids themselves differ in being rather indistinct in *Euchromadora*, where they are bordered by slightly raised fringes of cuticle, while in the other forms they are distinct with very prominent wide cuticular fringes round their edges.

In all the descriptions of the cuticle that follow it must be remembered that the conditions are reversed roughly half way along the length of the body. Thus when anteriorly directed processes are described as occurring within the cuticle on the anterior end of the body, those on the posterior half of the body will be directed posteriorly.

Finally in all the descriptions of the cuticle the modifications referred to are represented by a dense, dark component lying within the cuticle and embedded in a less distinct matrix. This dense component is generally in the form of transverse annules which, in longitudinal section, are roughly rectangular with the short side of the rectangle lying parallel to the antero-posterior axis of the body. (Text-figs. 60, 67, 69.)

EUCHROMADORA de Man, 1886

It is usual to defer using new names for taxa until the evidence on which the taxa are based has been presented. Here there are so many changes in nomenclature and so much discussion of evidence that to do so would make the entire presentation even more complicated than it already is, or will become. I shall, therefore, present the argument and evidence under various headings, usually the name of the genus I finish by delimiting.

The genus which is central to the morphological argument is *Euchromadora* which I consider first.

Head Structure

The immediate result of the detailed study of the structure of the head and oesophastome is to suggest that it is of little value in delimiting species within the genus. One difficulty is the technical problem imposed by the small size of some of the specimens and another is that the appearance of the dentition varies dependent upon the degree to which the month is open or closed. The following features are, however, common to all the specimens, of all the species studied.

There is always a row of denticles along the dorsal edge of the oesopharhabdion anterior to the large, solid dorsal onchium which is usually obviously bent about its mid-length. The anterior edge of the oesophastome is always developed as an anteriorly directed process on the most dorsal edge of the lateral wall of the oesophastome, and sometimes a similar development appears to be present on the lateral edges of the dorsal wall also.

The lateral and ventral walls of the oesophastome are always distinct and the lateral bear at least four rows of transversely arranged small solid cuticular denticles of which the most posterior (i.e. those lying deepest or most posterior within the oesophastome), Row-IV, tend to be largest and generally arise from a common thickened cuticular base or ridge. In some species the distribution of the denticles on the lateral walls appears to be characteristic but it is impossible to be sure as yet. Nevertheless there is almost invariably what looks like a swollen pad bearing two fairly prominent denticles with, frequently, a few smaller denticles between them, on the extreme anterior limit of the lateral wall (Row-I) with, posterior to this level, a further two rows, Rows II and III, anterior to the most posterior Row-IV.

The distribution of the denticles on the ventral walls of the oesophastome appears to be a little more valuable in delimiting species but here also some uncertainty remains. The anterior limit of each of the ventral walls is frequently obvious in *en face* views as a distinct curved rod-like ridge. This is followed more deeply, or posteriorly, by a number of small solid denticles with, at the extreme posterior depth of the oesophastome, a number (usually three) of large solid tooth-like structures which arise, typically, from a massive plate (Text-figs. 9, 10).

In detail the dentition in the various species I have studied is as follows.

Euchromadora vulgaris (Text-figs. 1–5).

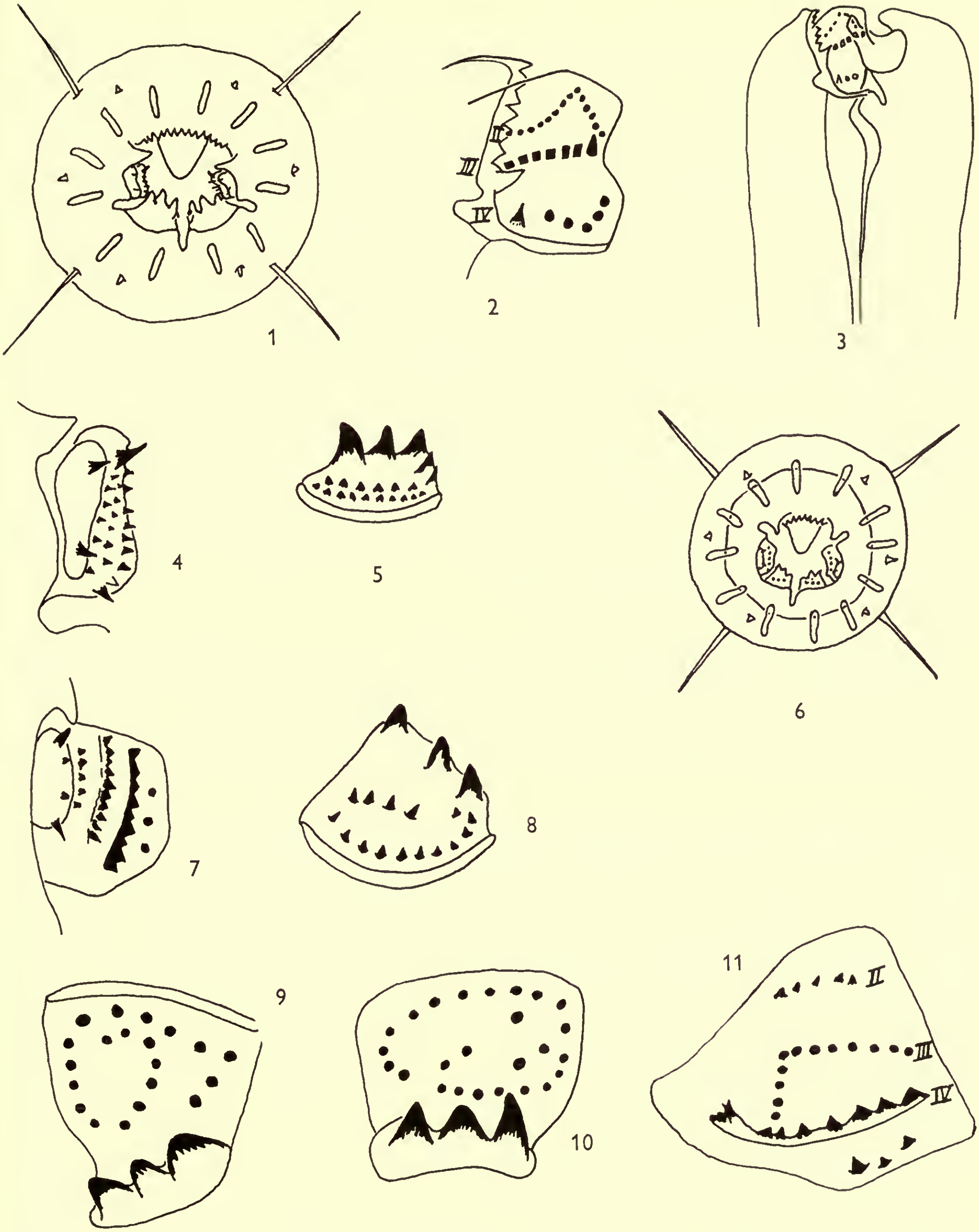
Lateral walls. Row-I: two large denticles, no smaller ones seen; Row-II: denticles small, row bent anteriorly (Text-fig. 2); Row-III: straight and prominent with most dorsal denticles larger than others; Row-IV: denticles prominent, row slightly L-shaped, largest most ventral (Text-figs. 2, 4).

Ventral walls. There are two rows of small denticles near the anterior edge, three very prominent and massive denticles posteriorly (i.e. deep within oesophastome) which arise from a distinct plate and one or two prominent denticles on the edge of the wall where it meets the ventral extension of the lumen. These denticles vary in appearance, possibly because of different angles of examination.

This description, based on light microscope studies, has been confirmed by electron scan (Stereoscan) examination.

Figs 1–11—*contd.*

gaulica. 6. *En face* view of head. 7. Lateral oesophastomal dentition, *en face* (sketch), dorsal towards top. 8. Left ventral dentition of oesophastome *en face* (sketch). 9–10. Inner views of ventral walls of oesophastome on one specimen. Ventral extension of oesophastomal lumen lies between figures. 11. Lateral dentition of oesophastome viewed from inner surface, dorsal to left.



FIGS. 1–11. 1–5. *Euchromadora vulgaris.* 1. *En face* view of head. 2. Oesophastomal dentition (sketch, detail). 3. Lateral view of anterior end of oesophagus, dorsal to right. 4. Lateral dentition of oesophastome *en face* (sketch), dorsal towards top. 5. Left ventral dentition of oesophastome *en face* (sketch). 6–11. *Euchromadora*

Euchromadora gaulica (Text-figs. 6–11).

Lateral walls. Row-I: tiny denticles between large dorsal and ventral denticles; Row-II: short, straight with tiny denticles; Row-III: L-shaped with short leg directed posteriorly and long leg transversely; Row-IV: very prominent with denticles arising from a distinct, curved, basal flange. In addition there are a number (three seen) of thorn-like denticles arising from the most posterior level of the wall. I am not absolutely certain but these latter structures appear to be additional to the more usual four rows of denticles. (Note that in Text-fig. 11 the ventral surface of the body is towards the right and the drawing shows the inner surface of the wall.)

Ventral walls. The small anterior denticles are arranged in a crude spiral (Text-figs. 8, 9. 10) while there are three massive, basal onchia arising from a very prominent plate. Three illustrations of the conditions are given of which Text-fig. 8 is taken fully *en face*, while Text-figs. 9 and 10 show the two ventral walls of one specimen. In this latter case the walls are viewed from the inner surface and are taken from a wholly dissected specimen. Text-fig. 9 shows the left wall and Text-fig. 10 the right. It should be noted that the spiral of denticles occurs towards the lateral surface of the body. In other words the right-hand side of Text-fig. 8 corresponds to the median ventral extension of the lumen while the left-hand side is contiguous with the lateral wall of the oesophastome.

Euchromadora striata (Text-figs. 12–24).

Lateral walls. Row-I: usual two prominent denticles with series of smaller denticles between them; Row-II: curves anteriorly and all denticles are about same size; Row-III: very slightly bowed anteriorly, denticles all about same size; Row-IV: denticles relatively massive, few in number and arising from very prominent basal plate.

Ventral walls. The occurrence of some variation could be established possibly because of the relatively large size of specimens of this species. The small, anterior denticles lie in three rows of which those of the most anterior row are consistently smaller than those of the others. In addition a varying number of tiny denticles can occur (or be seen) in some specimens but these are always restricted to the more lateral region of the wall (Text-figs. 14, 20). There are two, sometimes three, large denticles deep on the ventral wall of which two are consistently present near the edge of the ventral lumen (Text-figs. 15, 20). This may vary because of the contraction of the mouth opening so that in some specimens the large denticles are not quite on the edge (Text-figs. 14, 16). The large posterior onchia are very obvious in lateral view (Text-figs. 19, 24).

Euchromadora eileenae (Text-figs. 31–37).

The dentition of the oesophastome in this species is very similar to that in *E. gaulica*.

Lateral walls. All rows of denticles slope posteriorly from dorsal side (Text-fig. 34). Row-I: two prominent denticles only; Row-II: relatively few, small denticles in an almost straight line; Row-III: rather short and slightly bowed anteriorly; Row-IV:

straight, denticles prominent of which most dorsal is larger than the remainder, all arise from a definite plate, at least in one specimen studied *en face* (Text-fig. 37). Posterior to Row-IV are two, sometimes three, prominent dorsal edge of the walls.

Ventral walls. The denticles form a definite curved or spiral arrangement with the spiral towards the lateral surface of the body. Towards the mid-ventral extension of the lumen there are two large denticles but there does not appear to be any definite plate associated with them (Text-fig. 36) nor are they always present, or at least have not always been seen (Text-fig. 35).

Cuticle Structure

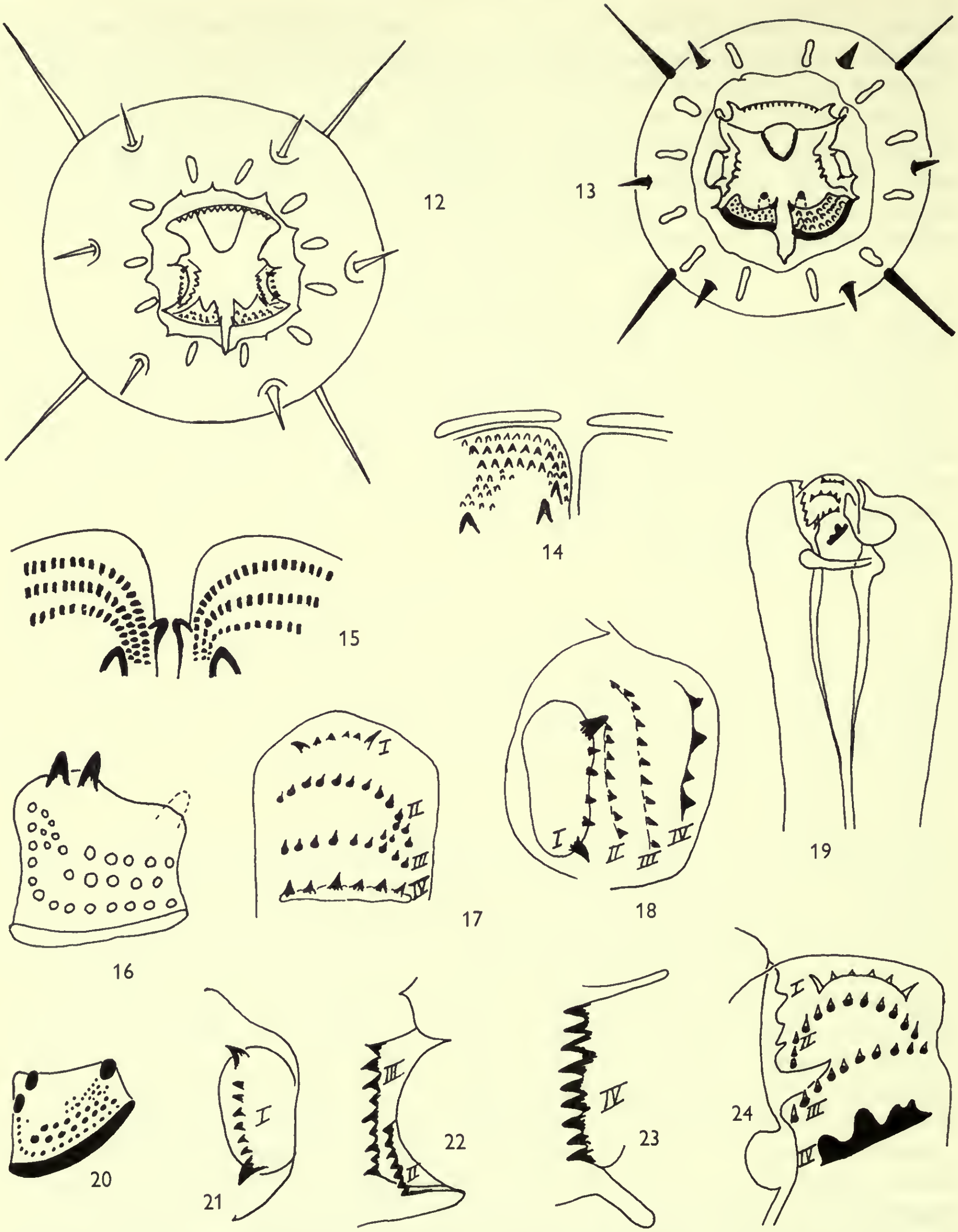
The detailed structure of the massively punctate cuticle occurring over the anterior region of the body in *Euchromadora* has been described elsewhere (Inglis, 1964) but, because at that time I was only considering the modifications of the punctation system, the structure of the unpunctate cuticle was not discussed nor were the lateral plates considered. Briefly, the cuticle consists of a series of annules of dense material embedded in a general covering of less dense material and all the structure usually described as cuticular modification or simply as cuticular structures are represented by these dense components.

Each annule is represented on the surface of the cuticle by a transverse striation and the annules themselves can be extremely complicated. At the anterior end of the body each annule can be thought of as composed of three subsiduary annules which together form a somewhat rectangular block in longitudinal section (Text-fig. 60). The outermost sub-annule is developed anteriorly as a thin, wedge-shaped flange which lies over the posterior edge of the next most anterior annule and posteriorly is curved to form a region covered by the flange from the anterior edge of the next most posterior annule.

The innermost sub-annule is more regularly rectangular in longitudinal section but from about the middle of the oesophagus length posteriorly it bears a lateral peg or plate which projects anteriorly to lie under the next annule anteriorly. There is a slight concavity on the posterior edge of this innermost sub-annule, immediately posterior to the anteriorly directed peg, into which the anteriorly directed peg from the next more posterior annule fits. These pegs I have called " lateral plates " and it should be noted that they lie within the lateral chords of the hypodermis and are below the lateral rod-like punctations when the cuticle is viewed from the surface (Text-figs. 60–61).

In some specimens the lateral plates appear to be represented by a series of granules of dense material but it is uncertain whether or not this is due to studying pegs in optical section as I have not had sufficient specimens to warrant treating them with sodium hypochlorite. It may be noted in passing that this is not the system to which Steiner (1918) refers, as he is dealing with the true punctation rods which lie above the lateral plates and that Wieser & Hopper (1967) appear to have confused the two sets of structures in their discussion of *Euchromadora gaulica*.

The massive punctation blocks arise from the region between the outermost and innermost sub-annules and can be pictured as a third sub-annule. These blocks which are circular in transverse section project anteriorly on the anterior half of the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FIGS. 12–24. *Euchromadora striata.* 12. *En face* view of head. 13. *En face* view of head of another specimen. 14. Dorsal-oblique view of inner surface of ventral oesophastomal walls (sketch). 15. As fig. 14, but extremely regular condition with only two large onchia (sketch). 16. Right ventral wall of oesophastome *en face* (sketch). 17. Inner surface of lateral wall of oesophastome, dorsal to left (sketch). 18. Right ventral, wall of oesophastome *en face* (sketch), dorsal towards top. 19. Lateral view of body to lie between the similar blocks developed on the next most anterior annule. The blocks are further connected to both the outermost sub-annule and the innermost over their posterior halves as I have illustrated elsewhere (Inglis, 1964, Figs. 13, 15). The conditions described above apply to the anterior half of the body Over the posterior half the conditions are reversed so that the outer sub-annules are extended posteriorly instead of anteriorly and the punctation blocks and lateral plates are also directed posteriorly instead of anteriorly.

To revert to the anterior cuticle, the large punctations disappear over two strips both dorsally and ventrally so that a V-shaped strip of punctations projects posteriorly along the dorsal and ventral surfaces of the body (see Coles (1965) particularly Fig. 1), until by about the posterior end of the oesophagus the dorsal and ventral cuticle is marked only by transverse striations. Meanwhile the large elongate punctations become slimmer and longer and are restricted to a fairly narrow zone running down the lateral surfaces of the body (Text-figs. 60–63).

The structure of the cuticle in *Euchromadora vulgaris* has been studied by light and electron microscopy by Watson (1965) but most of what she reports is based on an examination of the dorsal or ventral region of non-punctate cuticle. This explains the apparent discrepancy referred to by Lee (1966). In particular Watson describes the middle layer in this non-punctate region as consisting of overlapping plates, with which I agree, but it is the origins of these plate-like structures (a description which only applies to the view in longitudinal section) which is particularly interesting.

The lateral surface cuticle is relatively thick and is marked by the obvious punctations which correspond to the layer of rods sandwiched between the two other layers like teeth of a comb (Text-figs. 60, 65). Dorsally and ventrally the cuticle, which lacks such punctations, is much thinner. Each annule, in longitudinal section, is a thin wedge-shape with the thinner edge outermost and overlying the next more anterior or posterior annule (Text-fig. 63). The region of transition between these two zones of modification is most interesting since it explains, among other things, some of the features of the cuticle described and illustrated by de Man (1886). Before describing this transition zone I should stress that I have only been able to confirm this detail in *E. vulgaris*, *E. gaulica* and *E. loricata*.

The change from the lateral region with long punctations to the dorsal and ventral region without such punctations occurs very sharply and involves (on the anterior end of the body) the displacement of the innermost sub-annule of the dense component of the cuticle posteriorly relative to the remainder of the annule. At about the same level the punctation sub-annule becomes solid and it also is displaced posteriorly, but not to the same extent as the innermost. The combination of these displacements is to produce a wide, thin wedge-shaped (in section) annule, so that although the annules only overlap each other slightly on the lateral surface of the cuticle

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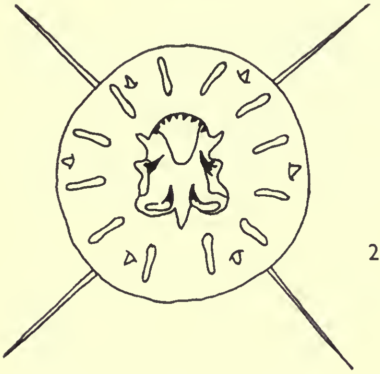
Figs. 12–24—*contd.*

anterior end of oesophagus, dorsal to right. 20. Right ventral wall of oesophastome *en face* (sketch). 21–23. *En face* optical sections through lateral wall of oesophastome, dorsal towards top (sketches). 21. Denticles of Row-I. 22. Denticles of Rows-II and III 23. Denticles of Row-IV. 24. Lateral wall of oesophastome viewed from outer surface (sketch), dorsal to right.

the overlap is considerable on the dorsal and ventral surfaces (Text-figs. 60–64). As a consequence each annule of dense material when considered alone is not a simple ring but is a narrow thick sector with punctation processes laterally and a thin, wide, wedged sector dorsally and ventrally. This is illustrated in a very simplified way in Text-fig. 65. One consequence of this relative displacement of the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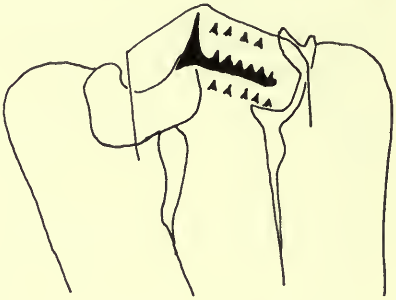
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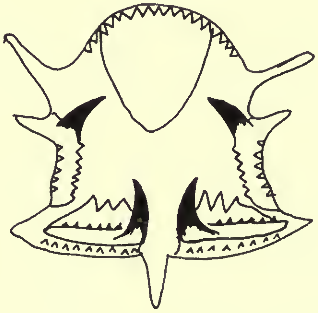
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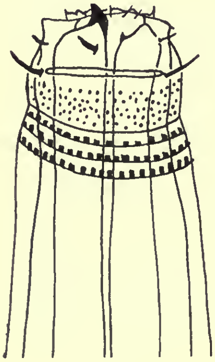
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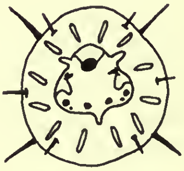
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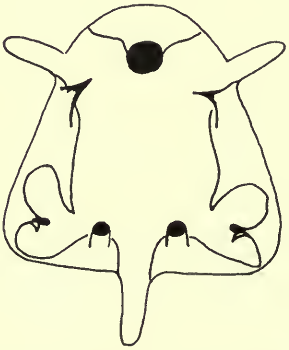
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Figs. 25–30. 25–27. *Steineridora loricata.* 25. *En face* view of head. 26. Lateral wall of oesophastome viewed from outer outer surface (sketch), dorsal to left. 27. *En face* detail of dentition of oesophastome (sketch). 28–30. *Graphonema georgei.* 28. Lateral view of anterior end of body. 29. *En face* view of head. 30. Oesophastomal dentition *en face* (sketch) dorsal towards top.

constituent sub-annules is that the analysis of the modification in whole mounts is very difficult because one edge of one sub-annule moves posteriorly relative to the others while the others, which can still be recognized in the specimen, remain at the same level. Over the whole diameter of the body the anterior edge of each annule remains at the same transverse level and appears as a straight striation running round the body. The general appearance of this cuticle is shown in Text-fig. 64, but it should be remembered that this illustration is taken from a much compressed specimen.

There are still some minor discrepances between this description and that given by Watson (1965), particularly the condition shown in her Fig. 3A in which are illustrated what she interprets as the " rod-like bodies " of de Man. However I suspect that what is shown is the anterior region just posterior to the amphids in which the cuticle is supported by rod-like punctations. This interpretation is supported by the fact that the cuticle shown in Fig. 3A is obviously considerably thinner than that shown in Watson: Fig. 1A which in turn is, I already know, considerably thinner than that in which the typical, massive punctation blocks or processes occur.

To complicate matters even further I suspect that the illustrations of the overlapping plate-like cuticle were taken from the transition zones at the anterior end of the body so that there are structures present which are definitely not present more posteriorly. I have, in fact, seen structures by the light microscope which resemble the transverse rings of dense material in Layer 1 in Watson's Fig. 2 but they cannot be analysed in my material. This feature deserves further study. Finally it is perhaps worth pointing out that the direct attachment of the muscles to the cuticle described by Watson is the feature responsible for the description of the basal layer by several other workers as longitudinally striated or with longitudinal fibres.

In view of these observations the genus may be rediagnosed thus:

EUCHROMADORA de Man, 1886

Chromadoridae: Cuticle: complex with large, prominent, elongate hexagonal or ovid punctations anteriorly and posteriorly which correspond to processes developed within cuticle from one side of each annule only; similar, but slimmer markings restricted to lateral surface over middle length of body; no punctations on dorsal or ventral surfaces over middle length of body; " lateral plates " generally well developed; no lateral differentiation.

HEAD: large, solid dorsal onchium preceeded by denticles on anterior dorsal edge of oesophastome; transverse rows of small, solid denticles on lateral walls of oesophastome; similar denticles anteriorly on ventral walls of oesophastome with, frequently, larger denticles posteriorly arising from a distinct plate; cephalic sense organs in three circles of which the outer is composed of four setae; mouth surrounded by twelve rugae; amphids elongate transverse slits without marked fringes of cuticle surrounding them; oesophagus without definite posterior bulb.

MALE: gubernaculum with prominent, generally hammer-shaped or L-shaped lateral pieces; no pre-cloacal supplements or other modifications of cuticle; tail relatively short and stout.

TYPE SPECIES: *Chromadora vulgaris* Bastian, 1865. Described above in part and reference confirmed by de Man's (1886) and Coles' (1965) descriptions in addition to the study of specimens.

OTHER SPECIES. The following species may be definitely referred to the genus *Euchromadora* as restricted by this diagnosis because they possess or appear to possess this combination of characters.

E. gaulica Inglis, 1962. Redescribed above in part. The gubernaculum has been re-examined in European specimens and the presence of the two minute denticles near the posterior end which are figured and described by Wieser and Hopper (1967) has been confirmed.

E. striata (Eberth, 1863). Redescribed below, page 191).

E. meadi Wieser & Hopper, 1967. Retained on the basis of the original description.

E. permutabilis Wieser, 1954. Retained on the basis of the original description.

E. tokiokai Wieser, 1955. Retained on the basis of the original description.

E. eileenae sp. nov. Described below, page 193.

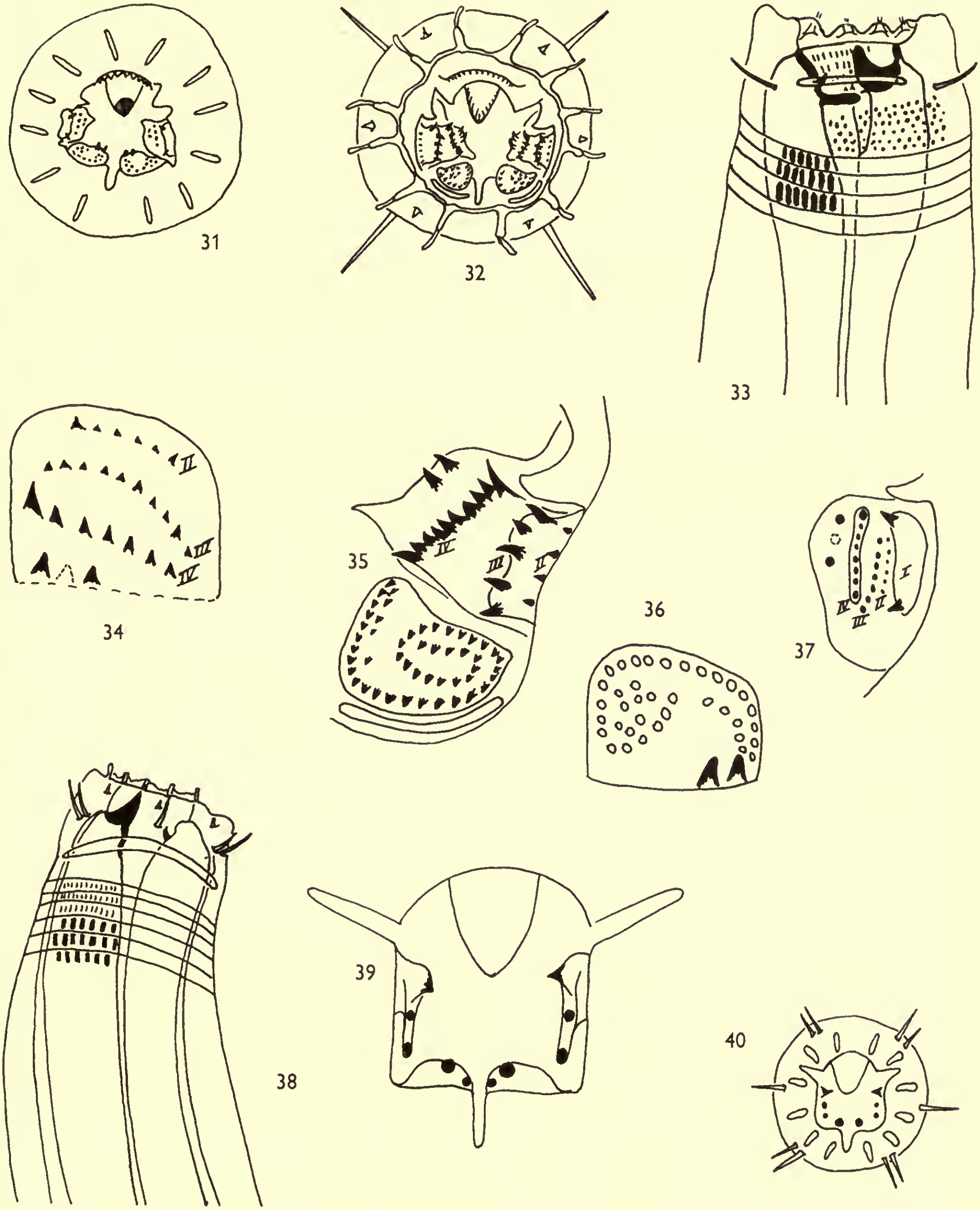
The disposition of other species usually referred to *Euchromadora* is listed on page 201.

STEINERIDORA gen. nov.

This new genus is proposed for some of those species which are generally referred to the genus *Euchromadora* but which differ most obviously from the species discussed above in possessing a distinct posterior oesophageal bulb. In this group are seven nominal species: *E. archaica* Steiner & Hoeppli, 1926; *E. amokurae* (Ditlevsen, 1921) (although Ditlevsen points out that his illustration tends to exaggerate the oesophageal bulb); *E. loricata* (Steiner, 1916); *E. adriatica* (von Daday, 1901); *E. dubia* Steiner, 1918; *E. denticulata* Cobb, 1914 and *E. stateni* Allgén, 1930.

E. loricata, of which I have studied specimens in detail, differs from the typical non-bulbed *Euchromadora* species in several other morphological features, many of which were reported by Steiner and Hoeppli in 1926 in describing *E. archaica*. The punctations in the cuticle, which are processes exactly as in *Euchromadora*, remain much the same size over the whole length of the body in contradistinction to the condition in *Euchromadora* (s.s.) where they become markedly thinner and longer over the middle length of the body. This is, I think, what Steiner and Hoeppli mean when they describe the cuticle of *E. archaica* as " . . . rather undifferentiated structure compared with other species; . . ." (Steiner & Hoeppli, 1926, page 571). There are clear non-punctate regions running down the dorsal and ventral surfaces of the body.

The structure of the oesophastome is recognizably *Euchromadora*-like but, although the typical dorsal onchium is present preceded by a row of denticles along the anterior dorsal edge of the oesophastome, it is a characteristic square shape (Text-figs. 25–27). The dentition of the lateral and ventral walls of the oesophastome is also similar to that of *Euchromadora* species with at least three transverse rows of small denticles on the lateral walls (Text-fig. 26). However the lateral walls also bear very prominent, sickle-like dorsally directed cuticular onchia which arise from distinct



FIGS. 31–40. 31–37. *Euchromadora eileenae.* 31. *En face* view of head. 32. *En face* view of head from another specimen. 33. Lateral view of head. 34. Lateral dentition of oesophastome viewed from inner surface (sketch), dorsal to left. 35. Oesophastomal dentition *en face* (sketch) from specimen with mouth wide open, shown in fig. 32. 36. Inner surface of left ventral wall of specimen shown in fig. 31 (sketch). Note presence of large paired denticles and spiral arrangement of small denticles. 37. Lateral dentition of specimen illustrated in fig. 31 *en face* (sketch). 38–40. *Austranema alii.* 38. Anterior end of body. 39. Dentition of oesophastome *en face* (sketch). 40. *En face* view of head.

ridges, the edges of which bear very tiny onchia (Text-figs. 26, 27). This ridge, and associated minute denticles, represents the middle of the three lateral rows of denticles.

Ventrally a similar pair of sickle-like onchia occur near the ventral edges of the ventral walls and these also arise from distinct transverse blade-like ridges which bear minute denticles along their anterior edges (Text-fig. 27). In addition on the ventral walls there is, possibly, a row of very tiny denticles anterior to the basal flanges of the large onchia while there is a set of three large onchia fairly deep in the oesophastome which arise from a plate-like base, exactly as in some of the *Euchromadora* species.

The same dentition is illustrated and described by Steiner and Hoeppli (1926) for *E. archaica* and I have established that the same conditions occur in *E. adriatica*, so far as is possible in whole mounts from the lateral aspect.

I therefore propose to refer these species to a distinct genus:

STEINERIDORA gen. nov.

Chromadoridae: Cuticle: complex with relatively stout, elongate punctations anteriorly and posteriorly which correspond to processes developed within the cuticle from one side of each annule only; similar and equally large, punctations continue on lateral surfaces of cuticle only over the middle region of body; no punctations on dorsal and ventral surfaces over much of middle body length where each annule is wider than it is laterally; " lateral plates " poorly developed; no lateral differentiation.

HEAD: large, squarish, solid dorsal onchium; denticles on anterior, dorsal edge of oesophastome; rows of small denticles on both ventral and lateral walls of oesophastome and large, curved, horn-like onchia projecting into oesophastome; cephalic sense organs in three circles of which outer is composed for four setae; mouth surrounded by twelve rugae; amphids elongate, transverse slits, not bounded by prominent fringe of cuticle; oesophagus with definite posterior bulb.

MALE: gubernaculum with prominent L-shaped lateral pieces; no pre-cloacal supplements or other modifications of cuticle; tail relatively short and stout.

TYPE SPECIES: *Spilophora loricata* Steiner, 1916.

OTHER SPECIES: *S. adriatica* (von Daday, 1901); *S. archaica* (Steiner & Hoeppli, 1926); *S.* (?) *dubia* (Steiner, 1918) *sp. inq.*

The position of the remainder of the seven nominal species with a posterior bulb to the oesophagus is difficult to establish, largely because of the poverty of the original descriptions. However, *Spilophora amokurae* Ditlevsen, 1921 fairly clearly has a hollow dorsal onchium (Pl. 2, fig. 4 in Ditlevsen, 1921) and has a very extensive unmarked region of cuticle at the anterior end of the body (see further discussion below, page 182); *Euchromadora dubia* Steiner, 1918 is insufficiently described for any certain opinion to be reached but appears to be referable to *Steineridora* although only as a *species inquirendum*; *E. denticulata* Cobb, 1914 is poorly described but because it appears to have a hollow or hollow-type dorsal onchium and the intermediate circle of cephalic sense organs is setose it is not referable to either

Euchromadora or *Steineridora* (see below, page 188); *E. stateni* Allgén, 1930 is treated as a synonym of *E. denticulata* by Wieser (1954) but is better treated as a *species dubia* as suggested by Coles (1965). Nevertheless it should be noted that the illustration of the head shows that *E. stateni* is not referable to *Steineridora* nor to *Euchromadora* since it has a hollow-type anteriorly directed dorsal onchium, an intermediate circle of six setae and an extensive non-punctate region at the anterior end of the body.

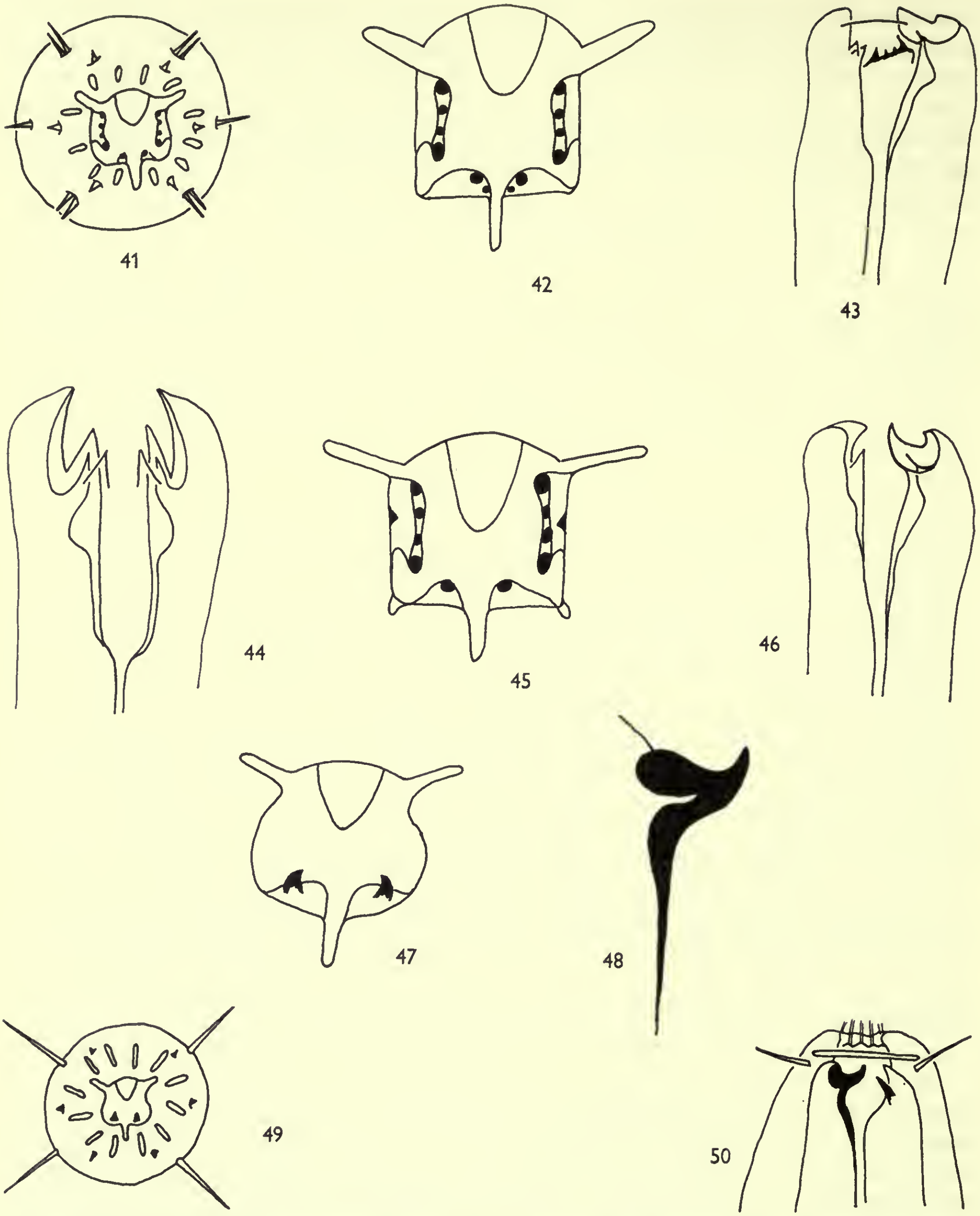
PARAPINNANEMA gen. nov.

In a new species from Western Australia, which is later named *Parapinnanema wilsoni*, the cuticle is thin and marked by a series of fine annules, in which there are fine elongate punctations, for about one head diameter posterior to the anterior end of the body. Posterior to this level the cuticle thickens very rapidly and is very prominently marked by obvious " battlement-like " punctations (Text-figs. 66, 97). The cuticle becomes thinner, rather slowly, over the posterior quarter of the length of the oesophagus and the markings become smaller and less pronounced but are still obviously battlement-like. Such a region of thick cuticle is a characteristic feature of most of the species in which the cuticle is battlement-like, although never as strongly as in *P. wilsoni* where it is one of the most startlingly obvious features of the species even under a low-power stereoscopic microscope (Text-fig. 97).

It should be noted that it is possible to get the impression that the cuticle is modified by a series of rods and dots over some areas but this depends upon the focusing and the extent to which the specimen being studied is under pressure. An additional complication in interpreting the structure of the cuticle from whole specimens is that, as in *Euchromadora*, each annule of the dense component of the cuticle consists of three or two sub-annules which are generally skewed so that one never lies immediately above another. As a result it is easy to interpret the conditions as representing two inner annules to each outer annule. This never appears to be true when the annules are separated by using sodium hypochlorite.

The punctation markings occur over the whole surface of the body, both dorsally and ventrally as well as laterally and the battlement-like markings become more pronounced again over the region just anterior to the cloacal opening or the anus and continue like this over the tail. The annulation is wide and the transverse striations on the surface of the cuticle are deep and pronounced (Text-figs. 73–75).

In detail the cuticle resembles *Euchromadora* in that each annule consists of two, or three (depending on interpretation) sub-annules of which the outermost is curved anteriorly (on the anterior half of the body) to form a strip overlying the posterior edge of the next immediately anterior annule. The innermost is similar to that in *Euchromadora*, consisting of a solid sub-annule which is slightly rounded along both the anterior and posterior edges. The major difference between the *Euchromadora* and *Parapinnanema* cuticles is that in the latter there are processes developed on both sides of the annules, on the middle of the body-length, about the middle of the thickness of the cuticle (Text-fig. 72), instead of on only one side as in *Euchromadora*, and there do not appear to be clear channels passing completely through the middle sub-annule.



Figs. 41–50. 41–43. *Austranema colesi*. 41. *En face* view of head. 42. Oesophastomal dentition *en face* (sketch). 43. Lateral view of anterior end of oesophagus, dorsal to right. 44–46. *Austranema shirleyae*. 44. Ventral view of oesophastome showing ventral onchia and lateral flanges in optical section (sketch). 45. Oesophastomal dentition *en face* (sketch). 46. Lateral view of anterior end of oesophagus, dorsal to right. 47–50. *Protochromadora scampae*. 47. Oesophastomal dentition *en face* (sketch) 48. Detail of dorsal onchium (sketch) 49. *En face* view of head. 50. Lateral view of anterior end of body.

This modification is apparent in a different way in the thick cuticle at the anterior end of the body where the battlement-like markings are very obvious. Here when the cuticle begins to become very thick the anterior edge of the outer annule becomes notched so that it looks like battlements. Along the posterior edge of the annule posteriorly directed peg-like processes are present which arise from the middle level of the annule (Text-fig. 67). In other words the annules are articulated together by a system derived from both the anterior and the posterior edges (see also Fig. 50b in Filipjev, 1918 and Fig. 52c).

As the cuticle becomes thinner posteriorly the dorso- and ventro-lateral articulating plates (see below) appear about halfway along the length of the oesophagus and the pegs on the posterior edges of the annules move relatively nearer the surface of the cuticle until the modfication is restricted to the outer surface of the cuticle. Meanwhile, as the middle pegs move outwards a series of grooves develop in the innermost sub-annule of the cuticle so that there are, in surface view, a series of large battlement-like modifications on the outer level and a series of very fine, short, elongate punctations on the innermost level of the cuticle (Text-figs. 68–71).

Posterior to the posterior end of the oesophagus the battlement-like modifications of the outer surface become smaller, and less distinct, until they almost disappear and are indistinct over roughly the middle third of the body length. At the same distance from the anterior end the fine striations of the inner sub-annule move relatively nearer the middle level of the cuticle as a series of anteriorly and posteriorly directed pegs (Text-fig. 72).

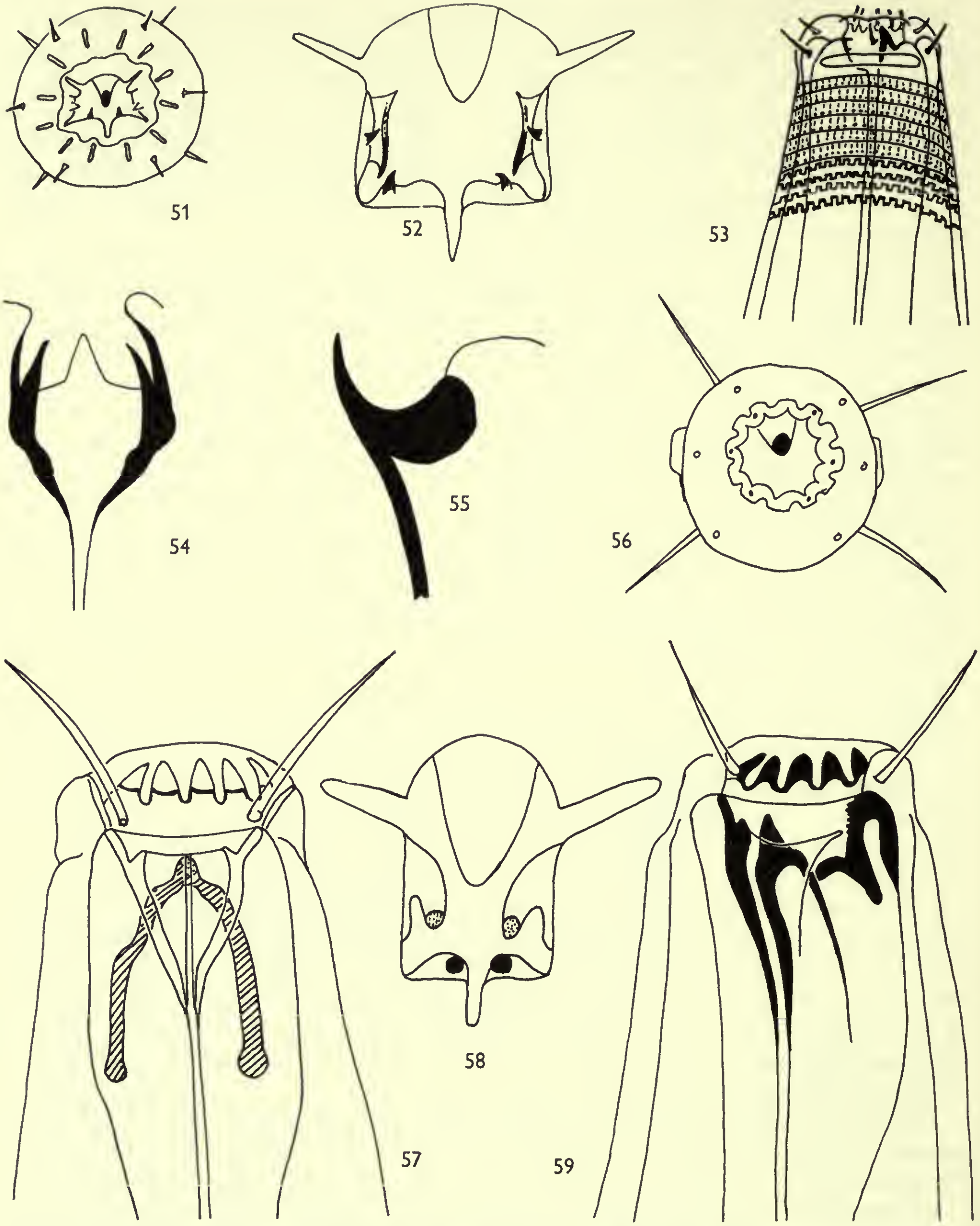
On passing further posteriorly the conditions are reversed; the middle layer of punctation pegs moves inwards to form fine elongate grooves on the inner sub-annules and the battlement-like indentations reappear on the outer surface and those along the *anterior* edge of each annule move inwards, relative to the surface of the cuticle, to form a series of pegs arising from the middle depth of each annule. In other words the conditions are reversed relative to those on the anterior part of the body.

At the level on the length of the body where the punctations are wholly due to the innermost modifications the annules are very skewed (Text-fig. 72) so that on focusing from the surface there appear to be two inner annules to each outer annule, and this condition reverses rather sharply about the middle of the body length. Over this same region of the body there is a distinct straight striation of the surface of the cuticle which runs round the middle of each annule and the annules are delimited anteriorly and posteriorly by wavy lines corresponding to the suppressed battlement-like processes (Text-fig. 75).

Therefore in contrast to the condition in *Euchromadora* there are two systems of punctation rods involved and the annules never widen dorsally and ventrally as in *Euchromadora*.

In addition to all this modification there are interlocking plates along the dorso- and ventro-lateral aspects of the body which are due to the development of interlocking extensions from the *innermost* level of the cuticle and are covered externally by the elongate punctations found on the rest of the cuticle (Text-fig. 68). The cuticle has no clear zones, without punctations, dorsally and ventrally.

The dorsal onchium is hollow (Text-figs. 53, 55) although in some specimens it is



FIGS. 51–59. 51–55. *Parapinnanema wilsoni*. 51. *En face* view of head. 52. Oesophastomal dentition *en face* (sketch). 53. Lateral view of head. 54. Dorsal view of oesophastome showing lateral flanges in optical section (sketch). 55. Detail of dorsal onchium (sketch). 56–59. *Hypodontolaimus slacksmithi*. 56. *En face* view of head. 57. Dorsal view of head. 58. Oesophastomal dentition *en face* (sketch). 59. Lateral view of head.

difficult to reach a decision. However, in addition to the structure of the cuticle and the form of the dorsal onchium, the specimens are characterized by no denticles along the anterior dorsal edge of the oesophastome, the intermediate circle of cephalic sense organs is setose, there are three circles of sense organs, the lateral walls of the oesophastome bear cuticular flanges which are not divided to form anteriorly directed denticles along their anterior edges so that each flange stands out in *en face* view as a simple, blade-like structure (Text-figs. 51–54). Ventrally there are two anteriorly directed cone-like denticles while in some specimens there appears to be a single denticle on the lateral walls of the oesophastome anterior to the lateral flanges (Text-figs. 51–53).

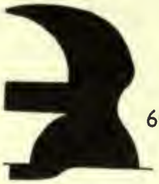
The tail is long and thin, the lateral pieces of the gubernaculum are L-shaped and there is a mid-ventral, thickened, pre-cloacal modification of the cuticle on the males as in *E. colesi* and *N. alii* (see Inglis, 1968 and Murphy, 1965).

The generic name *Odontocricus* Steiner, 1918 is already available for specimens with this massively battlemented type of cuticle. This name was proposed for a new species which was considered sufficiently distinct to warrant reference to a distinct subgenus of *Euchromadora*, *E.* (*O.*) *hupferi* Steiner, 1918. The remarkably obvious battlement-like structure of the cuticle is illustrated by Steiner (1918 : Fig. 4) but the species description is based on a juvenile female specimen and it is uncertain that it could ever be recognized again. Equally it is not possible to forecast the continuing uniqueness of the strongly battlemented cuticle so that rather than use a generic name of which the type species is a *species dubia* I propose to erect a new genus for the Australian specimens:

PARAPINNANEMA gen. nov.

Chromadoridae: Cuticle: without markings on anterior end until posterior to prominent amphids where a series of rods and dots appear; posterior to this level very prominent battlement-like appearance due to presence of processes within cuticle on both anterior and posterior edges of annulations; posterior to oesophagus, over most of body length, punctations slim and elongate but due to second inner layer, most outer layer now reduced to rather wavy lines on outer surface of cuticle; battlement-like cuticle reappears over posterior end of body from slightly anterior to anus or cloacal opening; annulation of cuticle very pronounced and wide; cuticle very thick over roughly length of oesophagus but region just posterior to head thin; no clear zones dorsally and ventrally and annules same width all round body; four files of articulating plates dorso- and ventrolaterally.

Head: slightly set-off by appearance of thin covering cuticle relative to conditions more posteriorly; dorsal onchium hollow; no denticles on anterior dorsal edge of oesophastome; flanges on lateral walls of oesophastome, without dentate anterior edges; one, solid, cone-like anteriorly directed onchium on each ventral sector at base of oesophastome; cephalic sense organs in three circles of which intermediate consists of six setae and outer of four setae; mouth surrounded by twelve rugae; amphids prominent transverse elongate slits bordered by prominent fringes of cuticle; oesophagus without prominent posterior bulb.



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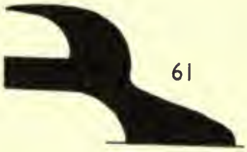

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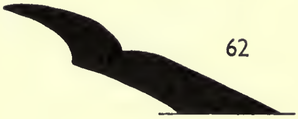

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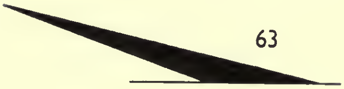

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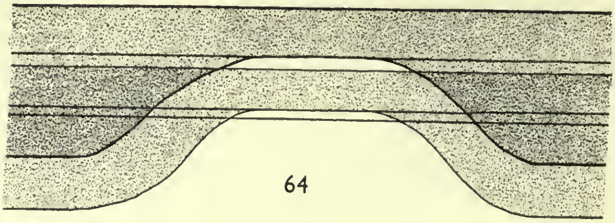

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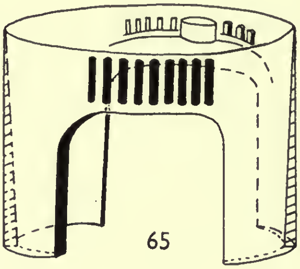

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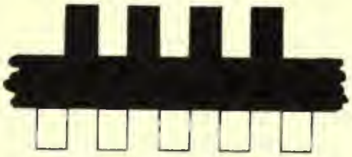

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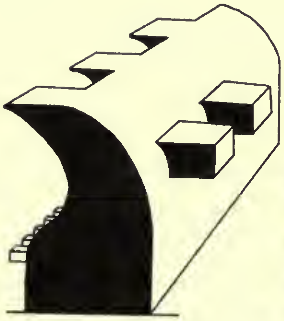

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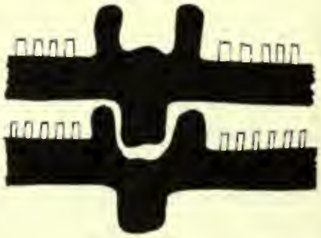

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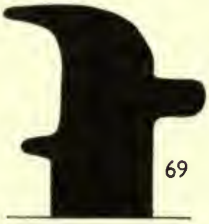

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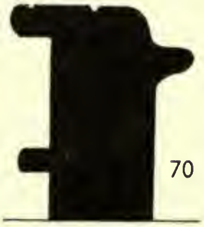

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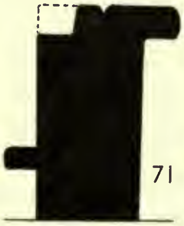

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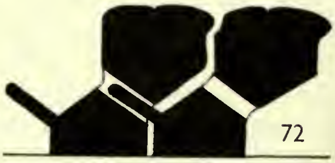

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FIGS. 60–72. Structure of cuticle. 60–65. *Euchromadora vulgaris*. 60–63. Successive longitudinal sections through one annule from wholly laterally to wholly ventrally or dorsally showing relative displacement of subannules. 64. Surface view of two annules showing relative displacement and widening of inner subannule. 65. Reconstruction of one annule about middle of body. 66–72. *Parapinnanema wilsoni*. 66. Anterior

MALE: gubernaculum with L-shaped lateral pieces; elongate, narrow, thickened. mid-ventral pre-cloacal cuticular modification; tail long and slim.

TYPE SPECIES: *Parapinnanema wilsoni* sp. nov.

PROTOCHROMADORA gen. nov.

Euchromadora scampae Coles, 1965 is characterized by an intermediate circle of six non-setase cephalic sense organs and four setae in the outer circle. The dorsal onchium is apparently hollow in some specimens and apparently solid in others (Text-figs. 48, 50). However the oesophastome has no denticles along the anterior dorsal edge, there are two ventral cone-like onchia and there is no trace of any lateral oesophastomal modification of any kind, neither in the forms of transverse rows of denticles nor as lateral flanges (Text-fig. 47).

The cuticle just posterior to the outer circle of cephalic sense organs is marked by tiny, slightly elongate, punctations which become more prominent posteriorly. They are large oval punctations over the anterior half of the length of the oesophagus which lie directly within the annulations. In other words, on focusing down through the annules the punctations lie directly over the inner sub-annules and wholly below the outer sub-annules so that there is no appearance of movement.

The punctation blocks are not, however, simple in structure since on focusing through them, from the surface, they become somewhat dumb-bell-shaped in section and finally at the deepest level are battlement-like in appearance (Text-figs. 76–79). The punctation blocks become slimmer on studying them more posteriorly and become much less prominent, very slim and close together. At the same time they begin to project from the anterior edge of each annule. As this projection becomes more pronounced notches appear in the posterior edges of each annulation to accept the processes projecting from the next more posterior annule (Text-figs. 77, 78). These notches on the posterior edge become deeper and more pronounced until the annules appear to be battlemented on both their edges (Text-fig. 79) with a distinct transverse striation running between them. I am not certain at which level these punctations lie within the cuticle but those on the anterior end appear due to processes in the middle depth while those on the middle of the body appear to be due to indentations on the extreme outer subannule of the cuticle (Text-fig. 79).

The conditions are reversed over the posterior half of the body.

Tiny lateral plates are present starting on the anterior end of the body about the

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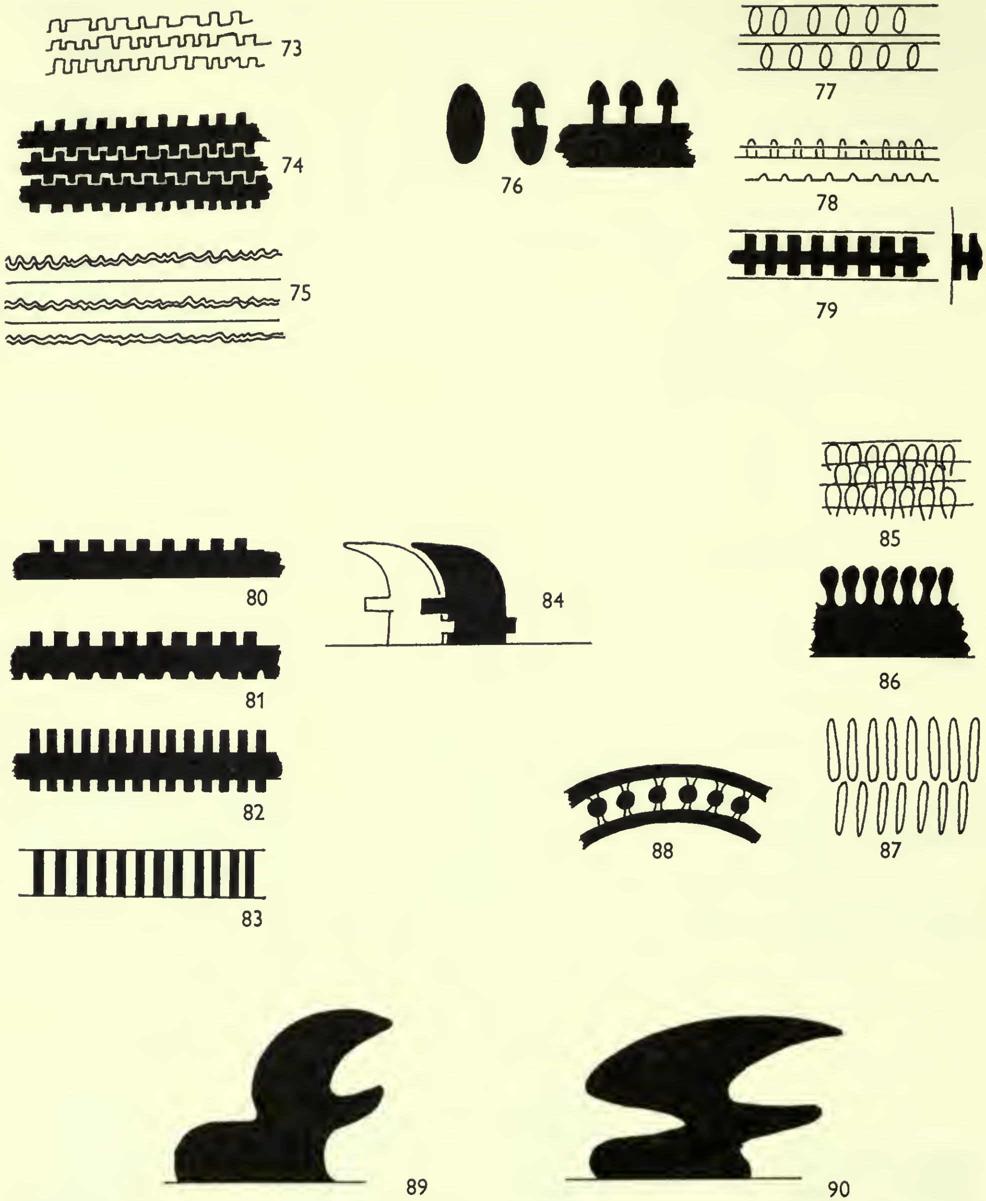
FIGS. 60–72—*contd.*

end of body, surface view. Black region is outer surface, white processes lie inwards. 67. Reconstruction of anterior annule. 68. Dorso- and ventro-lateral articulating processes. 69–72. Annules in longitudinal section, anterior to left. 69. Thick cuticle over anterior region of oesophagus. 70. Middle of oesophagus length, posterior process displaced outwards. 71. Posterior end of oesophagus. posterior process now on outer surface, anterior processes replaced by grooves on anterior edge. 72. One-third of body length from anterior end. Note distortion of annules with dominance of inner system of processes; outer processes reduced to irregularities on outer edges of annules.



FIGS. 73–90. 73–75. *Parapinnanema wilsoni*: surface appearance of cuticle. Anterior end towards top. 73. Just posterior to amphids. 74. Over oesophagus length. 75. On most of body posterior to oesophagus. 76–79. *Protochromadora scampae*: cuticle. 76. Punctation just posterior to amphids. From left to right: surface, about middle level, deep view (see description, page 177). 77. Just posterior to amphids. 78. Over first quarter of oesophagus. 79. Over most of body, plan on left, longitudinal section on right. 80–84. *Graphonema georgei*: surface appearance of cuticle. 80. Just posterior to amphids. 81. Three annules posterior to 80. 82. First third of oesophagus

level of the middle of the length of the oesophagus but over the middle region of the body they are represented by a series of granulations lying between the innermost parts of the dense annules of the cuticle.

The cuticle is marked by punctations laterally, but is clear dorsally and ventrally over the middle length of the body. In the male there is no precloacal mid-ventral modification of the cuticle and the tail is relatively short and stout.

This species is obviously distinct from those grouped in the genera *Euchromadora* and *Steineridora* and I propose to refer it to a new genus the validity of which will become clearer below.

PROTOCHROMADORA gen. nov.

Chromadoridae:: CUTICLE: complex with large, prominent, elongate punctations anteriorly and posteriorly which appear to correspond to processes developed on one side of each annule only; similar, but slimmer, punctations restricted to lateral surfaces of body over much of middle length; cuticle without punctations dorsally and ventrally over similar middle length of body; " lateral plates " represented by granules.

HEAD: dorsal onchium possibly solid but impossible to classify rigidly; no denticles on anterior dorsal edge of oesophastome; no denticles or flanges or any other structures on lateral walls of oesophastome; one cone-like, anteriorly directed onchium on each ventral sector at base of oesophastome; cephalic sense organs in three circles of which outer consists of four setae; mouth surrounded by twelve rugae; amphids elongate, transverse slits, not bordered by prominent fringes of cuticle; oesophagus without prominent posterior bulb.

MALE: gubernaculum with L-shaped lateral pieces; no pre-cloacal supplements or other modification of cuticle; tail relatively short and stout.

TYPE SPECIES: *Euchromadora scampae* Coles, 1965.

OTHER SPECIES: *P. mediterranea* (Allgén, 1942); *P. parafricana* (Gerlach, 1958).

The reference of *E. mediterranea* Allgén 1942 to *Protochromadora* is based on a study of some specimens in a rather poor condition. Nevertheless it is possible to confirm their specific identity and to establish with a fair degree of certainty their similarities to *P. scampae*.

The inclusion of *Euchromadora parafricana* Gerlach, 1958 in *Protochromadora* is slightly less certain as it is based on the published description. Gerlach (1958) gives

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FIGS. 73–90—*contd.*

to first third of body length. 83. Remainder of body. 84. Longitudinal section, about level of figure 82. Anterior to left. 85–88. *Austranema shirleyae*: cuticle. 85. Surface appearance, anterior end of body. 86. Detail at same level as 85. 87. Body posterior to oesophagus. 88. Transverse section at same level as 87 showing origins of punctation processes. 89. Longitudinal section at anterior end. Note marked anterior displacement of outer subannule. 90. Longitudinal section about middle of body (anterior to right in 89 and 90).

two figures of the head, one of which shows a hollow dorsal onchium (Gerlach, Fig. 4a) while the other (4b) shows a possibly hollow or solid dorsal onchium, reflecting the difficulty of distinguishing between the two forms. In addition an intermediate and an outer circle of setae is shown in Fig. 4b while only an outer circle of four setae is shown in Fig. 4a. The tail is long and thin, there are no pre-cloacal modifications or supplements and the oesophagus does not end in a bulb. The illustrations of the cuticle suggest the condition in *P. scampae* and I refer *E. parafricana* to *Protochromadora* with little hesitation.

GRAPHONEMA Cobb, 1898

Graphonema Cobb, 1898 is, in some ways, the most distinctive genus which remains to be considered and was erected by Cobb (1898) for *G. vulgaris* Cobb, 1898 with a reference to a further forthcoming species, *G. pachyderma*, which was never described. *G. vulgaris* was based on specimens collected from algae and sea sand on the coasts of New South Wales and Victoria, Australia. In describing it Cobb specifically draws attention to the following points: " The conoid neck terminates in a truncate head, conspicuous because of a distinct constriction behind it, and because of the sudden diminution in size on it of the cuticular markings . . ."; " The six cephalic setae opposite the apex of the dorsal tooth, and the four sub-cephalic setae . . .". In addition he refers to a minute dorsal tooth; linear, arcuate spicules of equal width throughout their lengths; a gubernaculum with lateral pieces; no oesophageal bulb and no pre-cloacal supplements.

I have collected specimens from the west coast of Australia, described below, which conform to this description with very great accuracy in all respects, although they appear to represent a different species from that described by Cobb (1898). As a consequence it is possible to reassess the status and diagnosis of the genus *Graphonema*.

The genus is easily recognized because the head is, as reported by Cobb, distinctly set-off as a swollen, almost globular, region on which there are very fine dot-like punctations (Text-fig. 28). More posteriorly the cuticle becomes thicker over the region of the oesophagus but always remains relatively thin and delicate in appearance when compared to the conditions in *Euchromadora* and the other genera considered here. Nevertheless the annulation of the cuticle is fairly marked and obvious. The punctations at the anterior end of the body, just posterior to the swollen region, are of a definite battlement-like form although the battlement processes are small relative to the width of the annules from which they arise (Text-fig. 80). On passing posteriorly the processes rapidly increase in relative size and notches develop in the posterior edges of the annules of dense material (Text-fig. 81). By the level of the posterior end of the first third of the length of the oesophagus the annules bear a distinct system of double battlement-like processes. The processes on the anterior edge are longer and nearer the surface of the cuticle than those on the posterior edge (Text-figs. 82, 84). Over the whole of this region the annules of dense cuticular material are roughly rectangular in longitudinal section with slight flanges developed along their anterior edges (Text-fig. 84).

The double-battlement markings on the cuticle over the posterior two-thirds of the oesophagus continue over the region posterior to the oesophagus virtually unchanged until about one-third of the total body length from the anterior end of the body where the battlement-like processes on the posterior edge of the annules move relatively nearer the surface of the cuticle, the cuticle becomes thinner and the punctations now look like long thin blocks (Text-fig. 83).

There are four clear zones running down the cuticle on the dorso- and ventro-lateral aspects so that the cuticle is marked by punctations dorsally and ventrally along the whole length of the body. These punctations are thinner and less obvious than those occurring on the lateral surface of the body. In the males there is no mid-ventral pre-cloacal modification of the cuticle and the gubernaculum is small and slightly L-shaped.

The mouth opening is surrounded by the usual twelve rugae and the cephalic sense organs are in three distinct circles of which the members of the outermost two circles are setose (Text-fig. 29). The amphids are very prominent, transverse slits bordered by obvious thin fringes of cuticle which stand out from the general surface of the cuticle. The circles of cephalic setae are far apart and the members of the outer circle lie on the same level as the amphids which are themselves positioned relatively far posteriorly from the anterior end of the body.

The dorsal onchium is small, hollow, directed anteriorly and there are no denticles developed on the anterior dorsal edge of the oesophastome. Each of the lateral walls of the oesophastome bears a flange which projects anteriorly most markedly towards its dorsal edge so that it resembles an anteriorly directed onchium when the level of focus is high. However on focusing down through the head, in an *en face* preparation, the flange appears progressively. There are no distinct separate denticles or processes developed from the effectively continuous edge of the flange (Text-fig. 30).

Each ventral sector bears one fairly prominent cone-like onchium. There is another less prominent pair, each member of which arises from, or near to, the ventro-lateral corners of the oesophastomal funnel. These structures are definitely present (Text-fig. 30) and there is a possibility that each ends anteriorly as a double point. This cannot be established with certainty but when this head is studied *en face* the dentition of the oesophastome is immediately obvious as seven bright points of light (Text-fig. 29) of which one is large and dorsal (the dorsal, anteriorly pointing onchium), two fairly large are lateral in position (representing the anterior edges of the lateral flanges), and four occur in an almost straight line across the ventral wall of the oesophastome (the onchia on the ventral sectors and those arising from the ventral corners of the oesophastome). With more careful focusing and studying the less certain second points to the ventro-lateral onchia can be made out.

The oesophagus expands evenly posteriorly but there is no distinct posterior bulb. The tail is long and slim (Text-fig. 99).

These features conform so exactly to Cobb's verbal picture of *G. vulgaris* that there can be little doubt that we are dealing with a species which is at least congeneric. As a consequence it is possible to reassess the genus which is certainly distinct.

The discovery of unequivocable specimens of *Graphonema* has further taxonomic consequence since Wieser (1954) " . . . thinks I am able to revive Cobb's doubtful genus . . ." and refers four species to that genus while in 1959 he adds another four species of which two are new.

As a result the genus currently contains the following nine species in addition to the type species: *Chromadora sabangensis* Steiner, 1915; *Spilophora amokuroides* Allgén, 1927 (redescribed by Wieser, 1954); *Spilophora norvegica* Allgén, 1932; *Chromadora paraheterophya* Allgén, 1932; with *Spilophora pusilla* Allgén, 1947; *Chromadora suilla* Allgén, 1947 and *Chromadora spectabilis* Allgén, 1932 referred to the synonymy of these species (Wieser, 1954); in 1959 Wieser adds the following species: *G. flaccida* Wieser, 1959; *G. clivosa* Wieser, 1959; *Chromadora tentabunda* de Man, 1890; *Chromadorita crassa* Timm, 1952 and *Chromadorita chitwoodi* Wieser, 1954.

However of these species *Chromadora tentabunda*, which is redescribed by Gerlach (1951), has a simple gubernaculum without L-shaped lateral pieces, a post-oesophageal bulb, a prominent hollow dorsal onchium with a well developed dorsal expansion of the oesophagus associated with it, the head is not set off and the intermediate circle of cephalic sense organs is not setose. Timm's (1952) *Chromadorita crassa*, a new name for *C. tentabunda* of Chitwood (1951), is I agree with Wieser (1959) almost certainly de Man's species.

Both *G. flaccida* and *G. clivosa* have a similar combination of characters; the dorsal onchium is large and hollow, the intermediate cephalic sense organs are not setose, there is a posterior oesophageal bulb, the gubernaculum lacks lateral pieces and the heads are not set off.

Spilophora amokuroides Allgén, 1927 is redescribed by Wieser (1954) and referred to the genus *Graphonema* with *S. pusilla* Allgén, 1947 and *Chromadora suilla* Allgén, 1947 as synonyms. As Wieser (1954) points out, Allgén's descriptions of *S. amokuroides* and *S. pusilla* are " insufficient " and he later (Wieser, 1959) adds that the use of the name *S. amokuroides* for his redescription is " . . . hypothetical, since Allgén's inexact figures and descriptions could very well fit any species of this group." I concur and propose to rename *Graphonema amokuroides* of Wieser, 1954 and will treat all four of Allgén's species as *species dubia*.

Chromadora sabangensis Steiner, 1915 is referred to *Graphonema* by Wieser (1954) but is originally described from females which makes discussion difficult. The intermediate circle of sense organs is not setose, the dorsal onchium is small and hollow, the punctations on the anterior end of the body are very light or lacking, the punctations on the general surface are thin and elongate and the posterior end of the oesophagus does not form a distinct bulb. It is, at best, a *species inquirendum*.

Finally *Spilophora amokurae* Ditlevsen, 1921 as redescribed by Wieser (1954) under the name *Euchromadora amokurae* and according to the original description, has a clear zone of cuticle anteriorly, the dorsal onchium is hollow, the intermediate circle of cephalic sense organs appears to be setose, there is no report of any pre-cloacal modification of the cuticle on the ventral surface of the male, the lateral pieces of the gubernaculum are L-shaped, and the tail is long and slim. In many of these respects the species differs from those referred to *Euchromadora* and, although some doubt remains, it appears most probably referable to *Graphonema* as re-diagnosed.

The redescription of a *Graphonema* species, *sensu* Cobb, means that the species referred to that genus by Wieser are displaced and I propose to refer them to a new genus, *Innocuonema*. This new genus and *Graphonema* may be differentially diagnosed thus:

GRAPHONEMA Cobb, 1898

Chromadoridae: Cuticle: anterior end of body swollen, bulb-like without punctations anteriorly and with tiny dot-like punctations posteriorly; anterior punctations, just posterior to bulb region, prominent and battlement-like; more posteriorly punctations long and slim; punctations on both dorsal and ventral surfaces of body; dorso- and ventro-lateral strips of articulating processes.

Head: markedly set off as swollen, bulb-like region; dorsal onchium hollow; no denticles on anterior dorsal edge of oesophastome; flanges on lateral walls of oesophastome, without dentate anterior edges; two prominent, cone-like anteriorly directed onchia on each ventral sector at base of oesophastome; cephalic sense organs in three circles of which intermediate and outer are far apart and composed of setae; mouth surrounded by twelve rugae; amphids prominent transverse slits bounded by prominent fringes of cuticle; oesophagus without prominent posterior bulb;

Male: gubernaculum with poorly developed L-shaped lateral pieces; no pre-cloacal supplements or other modification of cuticle; tail long and slim.

Type species: *Graphonema vulgaris* Cobb, 1898.

Other species: *G. georgei* sp. nov.; *G. amokurae* (Ditlevsen, 1921).

INNOCUONEMA gen. nov.

Chromadoridae: Cuticle: punctations complex and obvious; no lateral differentiation; no other information available.

Head: head not set off as swollen region; dorsal onchium fairly obvious and hollow, with associated dorsal swelling of oesophagus; structure of oesophastome unknown; only outer circle of four sense organs setose; amphid not prominent; definite posterior oesophageal bulb.

Male: gubernaculum without prominent lateral pieces; no pre-cloacal supplements or other pre-cloacal modifications; tail long and slim.

Type species: *Graphonema flaccida* Wieser, 1959.

Other species: *I. clovosa* (Wieser, 1959); *I. tentabunda* (de Man, 1890); *I. chilensis nom nov pro Graphonema amokuroides* of Wieser, 1954 *non Spilophora amokuroides* Allgén, 1927.

The following species are considered *dubia*: *Chromadora suilla* Allgén, 1947; *C. paraheterophya* Allgén, 1932; *Spilophora norvegica* Allgén, 1932; *S. amokuroides* Allgén, 1927; *S. pusilla* Allgén, 1947 and *Chromadora spectabilis* Allgén, 1932.

NYGMATONCHUS Cobb in Cobb, 1933

Before considering the remaining *Euchromadora*-type species I have seen it is necessary to consider the delimitation and diagnosis of the genus *Nygmatonchus* Cobb in Cobb, 1933. This genus was erected with one contained species, *N. scriptus* Cobb in Cobb, 1933, which was described, without illustrations, by reference to the genus *Rhips* Cobb, 1920. Using a combination of the verbal description of *N. scriptus* and the illustrations of *Rhips ornata* Cobb, 1920 it is possible to establish the following characteristic features for *Nygmatonchus*. The dorsal onchium is small, hollow and anteriorly directed, the amphid is prominent with a double contour, the cuticle is complex with lateral differentiation and basket-work markings anteriorly but only dots about the middle of the body, the cephalic sense organs of the intermediate and outer circles are setose and lie at the same level, the oesophagus lacks a definite posterior bulb, the tail is long and slim, and there is possibly a region of raised pre-cloacal modification on the males (not mentioned by later authors).

Wieser (1954) describes a new species *N. fossiferus* but delimits *Nygmatonchus* as " Distinguished from *Neochromadora* by having ten instead of the usual four cephalic setae". As the descriptions in this paper show, such a condition obtains in a wide range of forms. Nevertheless Wieser's description agrees with that given by Cobb in Cobb (1933) fairly well although the amphid is not obviously like that of *Rhips*, and the gubernaculum is not obviously L-shaped as in *Rhips*, a condition suggested by Cobb in Cobb's description.

Andrassy (1959) describes what he considers to be a female of *Nygmatonchus scriptus* and although I consider it unestablished that it is referable to that species it is, nevertheless, recognizably the same genus. Here, also, the dorsal onchium is small and hollow, the intermediate and outer circles of setae occur at the same level, the amphid is prominent with a double contour, there is definite lateral differentiation of the cuticle, and the tail is long and slim. Most recently Gerlach (1967) describes a new species *N. minutus*, in which the cephalic setae are in two circles but which otherwise agrees with the diagnosis of the genus.

These characters may be summarized in a diagnosis as:

NYGMATONCHUS Cobb in Cobb, 1933

Chromadoridae: cuticle complex anteriorly, elongate punctations posteriorly on middle of body; distinct lateral differentiation; intermediate and outer circles of cephalic sense organs on one or two levels, setose; amphid prominent with double contour; oesophagus without definite posterior bulb; dorsal onchium small and hollow; tail long and slim.

MALE: pre-cloacal modification on male (?); gubernaculum not L-shaped.

TYPE SPECIES: *Nygmatonchus scriptus* Cobb in Cobb, 1933.

OTHER SPECIES: *N. fossiferus* Wieser, 1954; *N. bicornata* (Wieser, 1959) comb. nov.; *N. minutus* Gerlach, 1967.

The reference of the three latter species to the genus is slightly doubtful. Although the first appears to be a true member of the genus the illustration of the amphid given by Wieser (1954) does not match that described by Cobb since it is short and rather indistinct (compare Wieser's Fig. 141a of *N. fossiferus* with Fig. 142a of *Actinonema pachydermatum* Cobb, 1920 a much more *Rhyps*-like amphid), and Wieser, as Murphy (1965) points out, does not mention any pre-cloacal modification of the cuticle.

Neochromadora bicornata was described by Wieser (1959) from females only so that it is difficult to refer it to any genus with certainty, but here again the amphid is small and indistinct, and the cephalic sense organs of the intermediate and outer circles are setose. Nevertheless the structure of the cuticle appears to match that of *Nygmatonchus*, particularly when Andrassy's (1959) and Gerlach's (1967) illustrations are considered, and I will refer Wieser's species to *Nygmatonchus* as a provisional measure, at least until males have been described.

Murphy (1965) describes a new species *Nygmatonchus alii* of which he says " My species conforms so closely to Cobb's generic description that there is little room for doubt as to generic placement". (Murphy, 1965; page 208.) However, the discovery of several species with roughly the same combination of characters as *N. alii* raises difficulties since if Wieser's interpretation of *Nygmatonchus* is correct and his illustration of the gubernaculum accurate the genus is characterized, among other features, by a small *Neochromadora*-type gubernaculum while if Murphy is correct the gubernaculum is *Euchromadora*-like.

However Cobb in Cobb's (1933) description of *N. scriptus* does not say that the lateral pieces of the gubernaculum (telamons) resembles those of *Rhips* (which are L-shaped) which one might have expected in view of the other direct reference to that genus. I, therefore, continue to accept Wieser's (1954) interpretation of the genus and cannot accept that Murphy's species is referable to it, particularly as the lateral differentiation he illustrates is not lateral and does not suggest " wings " as mentioned by Cobb in Cobb (see below, page 200).

AUSTRANEMA gen. nov.

The remaining *Euchromadora*-like species I have studied are all characterized by the presence of flanges, developed from the lateral walls of the oesophastome, with dentate anterior edges; the cephalic setae are in one circle of ten and lie anterior to the level of the amphids; the amphids are wide and prominent with cuticular fringes; the dorsal onchium is generally hollow; the cuticle is thick over the oesophageal region of the body; the lateral pieces of the gubernaculum are L-shaped; the tail is long and slim; there is a region of pre-cloacal modification on the mid-ventral surface of the body in the form of a raised strip of cuticle; the cuticle is marked by punctations dorsally and ventrally; the posterior end of the oesophagus swells evenly but there is no distinct posterior bulb; there are no denticles along the dorsal anterior edge of the oesophastome and there are anteriorly directed, cone-like onchia ventrally within the oesophastome.

Nygmatonchus alii Murphy, 1965 falls neatly into this group and the only apparent discrepancies are that Murphy does not report any dentition on the anterior edge of the lateral flanges of the oesophastome, although he illustrates the presence of such flanges in optical section (Murphy, 1965, Fig. 1, D) and describes a definite lateral differentiation of the cuticle. However, I have a few specimens from Western Australia which appear to be indistinguishable from those described by Murphy and can establish that the lateral oesophastomal flanges are dentate and that there is no lateral differentiation. I suspect that Murphy has, instead, illustrated the dorso- and ventro-lateral files of articulating plates common on this kind of nematode.

Similarly a re-examination of the original specimens of *Euchromadora shirleyae* Coles, 1965 and *E. colesi* Inglis, 1968 shows them to have this combination of characters and, to that extent, cannot remain as members of the genus *Euchromadora* (The description of the cephalic sense organs of *E. colesi* in Inglis (1968) is wrong.) It may be stressed again that when the mouth opening is closed and the oesophastome somewhat collapsed, the dorsal onchium folds posteriorly upon itself and gives every appearance in lateral view of being solid. However, when the mouth is open and the dorsal onchium fully extended it is clearly hollow.

I have been able to study the cuticle in some detail in *E. colesi*, *E. shirleyae* and *N. alii*, and it is structurally the same in all three. The sole difference of note is that the punctation blocks are much larger and the cuticle is thicker in *E. shirleyae* than in *N. alii* and *E. colesi*. As a result most of the following description is based on *E. shirleyae*. The structure of the cuticle in these three species differs from that in all the other species described in this paper in that each annule of dense material, when studied in transverse section, is markedly skewed, even at the extreme anterior end of the body so that the outer sub-annule lies fairly far anterior to the innermost (Text-fig. 89). This condition continues over the whole length of the body with the conditions reversed on the posterior half, i.e. the outer sub-annule is then posterior relative to the innermost.

The cuticle for about one head diameter posterior to the anterior end is marked by simple, dot-like punctations and then elongate punctations appear which are, as usual, due to the presence of anteriorly directed processes lying in the middle level of the cuticle. Initially these punctation-blocks are restricted to the anterior edge of each annule to give the appearance of a battlement-like cuticle (Text-figs. 85, 86) but after only two or three annules the punctations become elongate rectangles when viewed from the surface (Text-fig. 87). When single annules are studied, however, the punctations do not lie as strips in one plane but appear to be higher anteriorly than they are posteriorly. This appears to be caused by the anterior half (approximately) of each punctation being produced by the anteriorly directed process while the posterior half is due to grooves in the innermost, relatively posterior, sub-annule (Text-fig. 89). The processes are, as in *Euchromadora*, circular in transverse section and, although completely free nearer their outer ends, attached to the surface sub-annule by a thin strip of cuticle while more posteriorly a second similar strip attaches them to the innermost sub-annule (Text-fig. 88). As a result there are channels running through each annule between the punctation processes which continue as grooves in the innermost sub-annule.

Steiner & Hoeppli (1926) create a new genus *Dicriconema*, for a new species *D. tenuis*, based on the study of ". . . an apparently young female . . ." from Japan. The genus was diagnosed largely on the structure of the cuticle and, although both Wieser (1954) and De Coninck (1965) treat it as a " solid toothed " form, the original authors give no explicit information about the structure of the dorsal onchium and their figure (Tafel 1, Fig. 1) suggests that it was in fact hollow. The description shows that the cuticle is marked by elongate punctations over the whole surface, except for dorso- and ventro-lateral strips, and it appears possible that they studied a specimen similar to those discussed here.

I prefer not to use the name *Dicriconema* because it is extremely doubtful that *D. tenuis* could ever be unequivocably recognized. The difficulty is that mentioned in discussing *Odontocricus*. It is not yet possible to be sure that the structure of the cuticle is always covariant with the same features of other parts of the animal and, even if this could be established, it is doubtful that *D. tenuis* could ever be anything other than a *species inquirenda*, as I propose to treat it. It therefore appears advisable, because fairly drastic changes are involved anyway, that the knot be cut by introducing a new name for a generic group containing *E. shirleyae*, *E. colesi*, *N. alii* and related species.

AUSTRANEMA gen. nov.

Chromadoridae: CUTICLE: small, elongate punctations anteriorly which are not obviously battlement-like on all specimens but which are due to processes within cuticle developed from both sides of annules; cuticular annules markedly skewed anteriorly and posteriorly; punctations present on dorsal and ventral surfaces, although sometimes slimmer than those laterally at same level; dorso- and ventro-lateral files of articulating processes;

HEAD: not obviously set off; dorsal onchium difficult to classify but usually hollow; no denticles along anterior dorsal edge of oesophastome; flanges on lateral walls of oesophastome with dentate anterior edges; prominent, cone-like, anteriorly directed onchia on ventral sectors at base of oesophastome; outer and intermediate circles of cephalic sense organs at same level, all setose; mouth surrounded by twelve rugae; amphids prominent, transverse slits bounded by prominent cuticular fringes; oesophagus without posterior bulb, but slightly expanded posteriorly.

MALES: gubernaculum with prominent L-shaped lateral pieces; mid-ventral, elongate, pre-cloacal modification present; tail long and slim.

TYPE SPECIES: *Euchromadora colesi* Inglis, 1968.

OTHER SPECIES: *A. shirleyae* (Coles, 1965); *A. alii* (Murphy, 1965); *A. pectinata* (Wieser & Hopper, 1967).

Euchromadora pectinata Wieser & Hopper, 1967 is described as having a pre-cloacal mid-ventral modification of the cuticle and an oesophagus with a dilated posterior end but no distinct bulb; but the intermediate circle of cephalic sense organs is papillose. I shall, therefore, refer it to *Austranema* because of the first two features and full confirmation must depend upon a re-examination of the specimens. It should be noted that Wieser & Hopper (1967) refer to the presence of a post-cloacal thickening of the cuticle. This kind of modification occurs in some specimens of all the species I have seen but does not appear to be consistent in its occurrence. Perhaps I have simply been unable to see it.

Euchromadora meadi Wieser & Hopper, 1967 is left in the genus *Euchromadora* although it looks suspiciously like a member of *Austranema*. Here again a re-examination of the specimens is called for.

Uncertain ***Euchromadora*** and ***Euchromadora***-like Species

Some nominal species which have been described as members of *Euchromadora* and some species which appear similar to the various genera recognized above remain to be considered. Some of these species may be easily dismissed because of poor descriptions but others have to be considered because the convergence demonstrated above makes their generic placement difficult or uncertain. In such cases there is little doubt that the species concerned could be recognized again but there is insufficient information at present to allow them to be referred to one or other of the *Euchromadora*-like genera recognized here.

Cobb (1914) describes four new species from the Antarctic, which he refers to *Euchromadora*. More recently two of them are referred to other genera by Wieser (1954): *E. antarctica* to *Prochromadorella* and *E. septentrionalis* to (?) *Hypodontolaimus*; while the other two *E. denticulata* and *E. meridiana*, are kept in *Euchromadora* as doubtful species which are treated as *species dubiae* by Coles (1965). While agreeing with this, it is worth pointing out that it is now clear that neither of these latter species is a *Euchromadora*-type. Both have " hollow " dorsal onchia, both have two circles of setae, both have very prominent amphids and both have extensive, non-punctate or lightly punctate regions anteriorly. Unfortunately the descriptions make it impossible to establish their relationships more fully and it remains doubtful that either could be recognized again.

A large number of nominal species of *Euchromadora* have been named, described, redescribed or reported by Allgén in a large number of publications. Some of these have been " recognized " and redescribed by other authors but the general standard of Allgén's work is so poor that many such redescriptions are based on guess work. The majority of Allgén's species have been treated as unrecognizable by several authors (summarized by Coles, 1965), and will not be reconsidered here.

Steiner (1918) describes five new species of *Euchromadora* all of which are best treated as *dubia*, as proposed by Coles (1965) who, however, treats *E. hupferi* as a *species inquirenda*. As argued above, although it is possible to recognize the genus to which this species should be referred it is most unlikely that the species could ever be recognized. As a consequence *E. hupferi* is also considered a *species dubia*.

It is worth noting that *E. longicaudata* Steiner, 1918, in which the amphid is prominent with, apparently, a double contour and a dorsal onchium which appears to be of the hollow-type, is referred to *Actinonema* by Wieser (1954). Wieser, nevertheless, points out that " the male genital apparatus of this species is insufficiently described but it clearly differs in structure from that of the following species."

(i.e. *A. pachydermatum* Cobb, 1920). This is certainly not true since Steiner only studied a female and naturally says nothing about the male and it is extremely unlikely that Steiner's species could be unequivocably recognized again or differentiated from other species of any genus to which it might be thought to belong.

Wieser's (1954) comment on *A. longicaudata* must refer to the descriptions of *Pareuchromadora fragilis* of Allgén, 1942 and *P. setifer* Schuurmans Stekhoven, 1943 both of which he refers to the synonymy of *E. longicaudata.* There is no obvious justification for any of this since *P. fragilis* is, like *E. longicaudata,* known only from a female while *P. setifer* is recognizably an *Actinonema* species. As a consequence I treat *E. longicaudatum* Steiner, 1918 as a *species dubia*; *P. fragilis* of Allgén, 1942 as a *species dubia* and recognize P. *setifer* as a *species inquirenda* and refer it to *Actinonema.*

Also in 1943 Schuurmans Stekhoven describes *Euchromadora inflatispiculum* which is clearly not referable to that genus and must remain a species *incertae sedis* until further specimens have been studied. From the descriptions it appears to have a hollow dorsal onchium and the redescription of Schuurmans Stekhoven (1950) does not appear to be the same species as that described in 1943, as is pointed out by both Wieser (1954) and Coles (1965).

Euchromadora arctica Filipjev, 1946 is a species with a hollow dorsal onchium, an oesophagus without a posterior bulb, with L-shaped lateral pieces to the gubernaculum, four cephalic setae, an extensive clear zone of cuticle at the anterior end of the body and, according to Filipjev (1946), there is a mid-ventral pre-cloacal papilla on the male. If this be correct the species is very different from any of the others described here or by others. In addition the form of the dorsal onchium is very cyatholaimid in appearance. As a result I propose to treat this species as *incertae sedis* although it shows some similarity to *Austranema.*

REMARKS ON THE CLASSIFICATION OF THE CHROMADORIDAE

Almost all discussion of the classification of free-living marine nematodes, in particular, and all non-parasitic forms in general, starts or finishes by stressing the doubtful value of much of the present grouping. Such comments are undoubtedly justified. The classification of the Family Chromadoridae is no exception and is probably as unreliable as that of any other family. Its limits and divisions float in a cloud of taxonomic uncertainty lightened only by flashes of morphological ignorance. As De Coninck says, "Toute la famille des Chromadoridae devra etre soigneusement révisée" (De Coninck, 1965, page 637.)

Although it is easy to offer destructive criticism of the classification, constructive suggestions are much more difficult to formulate because of our extensive lack of knowledge about the animals involved. The weakness of this position is well exemplified by the present work. It is only too clear that there is no sound basis on which to erect a classification; and there is no background of morphology against which to assess new information. The immediate consequence is that it is difficult to suggest easily observed characters or, more usefully, characters which have previously been described, which can be relied upon to be covariant with those structures of the head and cuticle described above.

The recognition of one group with a solid dorsal onchium and one with a hollow onchium is easy when the extreme and clear cut conditions are compared. The division is difficult, if not impossible, to apply when a solid " hollow " onchium is examined. Equally the two groups, so far as they have been studied, appear to differ in several covariant characters of the cuticle and dentition but it is difficult to apply this to those groups with simple punctate cuticles and we do not know, as yet, whether all the " hollow " toothed forms are similar in their other morphological characters. In other words it has been established that some " solid " toothed forms are, in other characters, most similar to " hollow " toothed but we do not yet know if forms which look obviously " hollow " toothed may not later be found to have great similarities with the obviously solid toothed.

In an attempt to overcome some of this uncertainty I have looked at a very small number of other species. In *Spilophorella paradoxa* (de Man, 1888), for example, there is obvious difficulty in describing the structure of the dorsal onchium. I would call it hollow but most groupings presuppose it is solid (e.g. Wieser, 1954; De Coninck, 1965). Be that as it may, there is a pair of small, ventral, anteriorly directed cone-like onchia in the oesophastome and there appear to be lateral flanges arising from the lateral oesopharhabdions. In these respects, therefore, *Spilophorella* falls into the hollow-toothed group of genera.

The conditions in *Hypodontolaimus* are much clearer, because the specimens of *H. slacksmithi* (described below) are relatively large. Here the mouth is surrounded by twelve, inwardly pointing, flanges developed from the wall of the cheilostome and there are no rugae as in typical Chromadoridae, the dorsal onchium is very prominent and hollow, there are no denticles along the dorsal anterior edge of the oesophastome, the oesophastome is rectangular in transverse section with two ventral, cone-like, anteriorly directed onchia on the ventral sectors and there are typical lateral flanges developed from the lateral walls of the oesophastome. These flanges are most anterior towards their ventral edges so that they look like pointed onchia on focusing up on *en face* preparations (Text-figs. 57–59).

In addition, in *Hypodontolaimus* the cuticle is of a battlement-type and a similar condition is suggested for various other " hollow " toothed species. For example Filipjev's (1918) illustrations of *Chromadora sabulicola* (Plate 8, fig. 50b) and *C. poecilosomoides* (Plate 8, figs. 52a, b, c) [both now referred to *Neochromadora*] show a battlement-like cuticle co-occurring with a hollow dorsal onchium. Equally many of Gerlach's (1951) illustrations show a similar association between a hollow onchium and a battlement-like cuticle.

To extrapolate, it appears that the presence of a hollow dorsal onchium is frequently associated with the presence of lateral flanges and cone-like ventral onchia in the oesophastome, and with the possession of a battlement-like modification of the dense component within the cuticle. There is, as yet, insufficient information on the structure of the cuticle and oesophastome in those species with an unequivocably solid dorsal onchium to allow any conclusions to be reached and the relationships of those species with simple punctate cuticles may always be difficult to establish. In spite of this uncertainty it appears that Wieser's (1954) treatment of the Chromadoridae in two groups distinguished crudely by the form of the dorsal onchium is of significance but it is doubtful that enough information yet exists to make De Coninck's (1965) division of the family into subfamilies on the same character acceptable.

For example there appear to be at least two distinct groupings possible for those genera in which the dorsal onchium is hollow. One of the groups consists of the genera considered above, which appears to culminate in a form such as *Parapinnanema wilsoni*, in which the cuticle is elaborate, thick and strong but the dorsal onchium is small. The other group contains those nematodes in which the dorsal onchium is very prominent and obviously hollow, frequently with a massive development of the oesophageal musculature associated with it, the cuticle is not thick, very elaborate and dark, and the gubernaculum is relatively simple. This group contains genera such as *Hypodontolaimus* and *Nygmatonchus*.

I would, therefore, expect that further study will lead to the recognition of at least three distinct groups within the subfamilies Chromadorinae and Hypodontolaiminae as recognized by De Coninck (1965). This does not, however, take into consideration those forms grouped by De Coninck in the Ethmolaiminae, Cyatholaimidae and even the Desmodoridae, the analysis of whose relationships is closely tied to the Chromadoridae. In all these groups there appear to be various independent lines of modification all of which lead to a stronger and more elaborate cuticle. As a result there is almost certainly a large amount of concealed convergence which is, as yet, unrecognized so that much of the current classification continues to be suspect.

DESCRIPTIVE SECTION

In agreement with the arguments of Wieser & Hopper (1967) I only give absolute measurements of specimens and have not given ratios.

Euchromadora striata (Eberth, 1863), Filipjer, 1918

(Text-figs. 12–24; 91–93)

Weed and associated hold-fasts and sand; silty and sheltered. In 60 cm. water. Cheyne Beach, Nr. Albany, W.A.

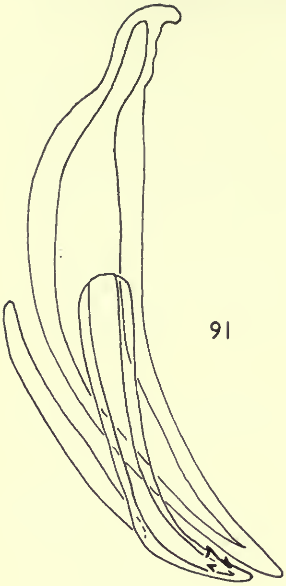
Weed and associated hold-fasts and sand; on exposed rocks. Goode Beach, Albany, W.A.

Weed and associated hold-fasts and sand; no silt, on exposed beach in 60 cm. water. Sarge Bay, Cape Leeuwin, W.A.

Among weed in rock pools. Robert Point, Mandurah, W.A.

Among weed on coral reef in 60 cm. water. Radar Reef, Rottnest Island, W.A. measurements (mm.).

MALES. Body length: 1·61; 1·64 ; 1·67; 1·86; 2·37. Body breadth: 0·078 0·078, 0·076; 0·068; 0·082. Diameter of head: 0·031; 0·030; 0·033; 0·033; 0·033. Length of cephalic setae: 0·009; 0·010; 0·011; 0·011; 0·011. Oesophagus length: 0·31; 0·33; 0·33; 0·35; 0·36. Length of spicules: 0·075; 0·083; 0·085; 0·085; 0·079. Gubernaculum length; 0·052; 0·047; 0·052; 0·048; 0·046. Tail length: 0·185; 0·238; 0·232; 0·212; 0·215. Cloacal diameter: 0·066; 0·057; 0·061; 0·052; 0·059.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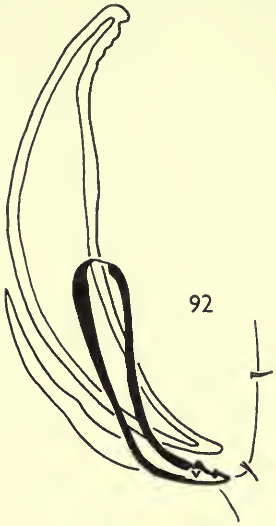
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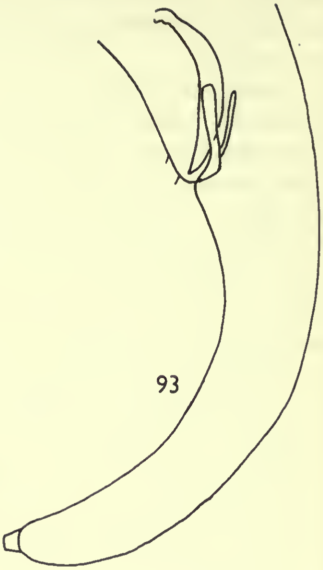
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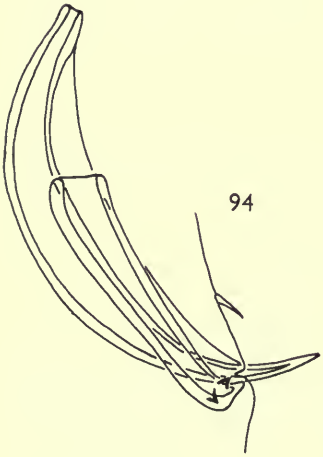
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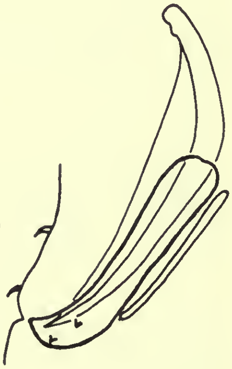
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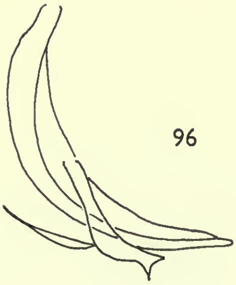
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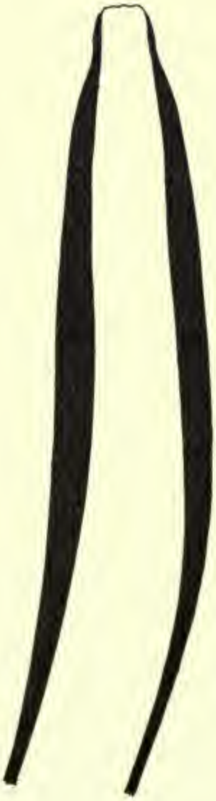
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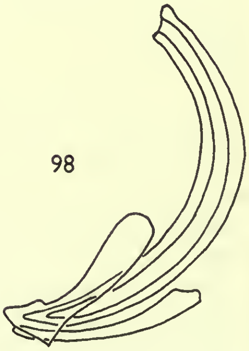
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FEMALES. Body length: 2·13; 2·16; 2·63. Body breadth: 0·110; 0·098; 0.131. Diameter of head: 0·036; 0·036; 0·037. Length cephalic setae: 0·013; 0·011; 0·013. Oesophagus length: 0·40; 0·39; 0·43. Tail length: 0·208; 0·221; 0·234. Distance of vulva from anterior end: 1·18; 1·09; 1·25. Size of eggs: 0·069 × 0·046; 0·073 × 0·063.

This species is the same as that described by Coles (1965) and Filipjev (1918) and it should be noted that Coles' figure of the spicules (Fig. 26) shows the spicules as rather too narrow posteriorly and the " serrated " posterior end to the lateral piece of the gubernaculum is three denticles (Text-figs. 91, 92) as in the Australian specimens.

The only major differences between the specimens from Australia and England are that the setae are slightly shorter in the Australian forms. The detailed structure of the head is described on page 162.

This species is wide-spread and common on the coasts of Western Australia and I have collected it from as far north as Perth, south down the coast to Cape Leeuwin and along the south coast as far as Cheyne Beach about 30 miles east of Albany.

Euchromadora eileenae sp. nov.

(Text-figs. 31–37; 94–95)

Weed on coral in 60–100 cm. water; Radar Reef, Strickland Bay, Rottnest, W.A. (Type locality).

Weed and sand brought up in trawl from 12 m.; Shark Bay (midway between Denham and Dirk Hartog Island), W.A.

Weed and sand associated with hold-fasts, silty, sheltered, in 60 cm. water. Cheyne Beach, Nr. Albany, W.A.

Measurements (mm.)

MALES. Body length: 1·63; 1·79; 1·96; 2·05. Body breadth: 0·048; 0·064; 0·062; 0·059. Diameter of head: 0·023; 0·026; 0·026; 0·024. Length of cephalic setae: 0·008; 0·009; 0·009; 0·008. Length of oesophagus: 0·269; 0·281; 0·316; 0·296. Spicule length: 0·049; 0·053; 0·058; 0·061. Gubernaculum length: 0·034; 0·035; 0·040; 0·038. Tail length : 0·225; 0·189; 0·221; 0·236. Cloacal diameter: 0·039; 0·043; 0·041; 0·044.

FEMALES: Body length: 1·74; 1·87; 1·93. Body breadth: 0·093; 0·089; 0·091. Diameter of head: 0·026; 0·029; 0·029. Length of cephalic setae: 0·009; 0·009; 0·10. Length of oesophagus: 0·310; 0·314; 0·326. Tail length: 0·188; 0·208; 0·223. Anal diameter; 0·039; 0·040; 0·043. Distance of vulva from anterior end of body: 0·88; 0·91; 0·97. Diameter of eggs (spherical): 0·047–0·049.

FIGS. 91–98. 91–93. *Euchromadora striata*. 91–92. Gubernaculum and spicules. 93. Lateral view of male tail. 94–95. *Euchromadora eileenae*. Gubernaculum and spicules. Difference in appearance due to different angles of view. 96. *Graphonema georgei*. Gubernaculum and spicules. 97–98. *Parapinnanema wilsoni*. 97. Anterior end of body. Black region is thick cuticle in section. 98. Gubernaculum and spicules.

The structure of the head is described on page 162 and the cuticle is typical of the genus. The lateral plates are tiny and a series of four files of longish setae occur over the oesophageal region of the body.

The lateral pieces of the gubernaculum are stout with a very slight ventral curve at the distal end. On this curved region are two tiny denticles. The spicules are slightly curved and bear alae. This detail of both the spicules and the gubernaculum has been confirmed by dissection and is difficult to establish from whole mounts.

E. eileenae differs from all other members of the genus in the shape of the lateral pieces of the gubernaculum in which the distal end is hardly L-shaped.

The species is fairly common on the coasts of Western Australia with a wide range from Shark Bay in the north to Cheyne Beach in the east, on the south coast.

Parapinnanema wilsoni gen. et sp. nov.

(Text-figs. 51–55; 66–72; 73–75; 97–98)

From weed and associated sand without silt, on exposed beach in 60 cm. water. Sarge Bay, Cape Leeuwin, W.A. (Type locality).

From among finger-like green algae in rock-pools, just east of Cape Naturaliste (Bunker Bay), Geographe Bay, W.A.

Measurements (mm.).

MALES. Body length: 1·34; 1·47; 1·50; 1·78. Body breadth: 0·039; 0·034; 0·044; 0·046. Head diameter: 0·016; 0·016; 0·016; 0·018. Length of cephalic setae: 0·007; 0·007; 0·008; 0·006. Oesophagus length: 0·23; 0·24; 0·29; 0·27. Length of spicules: 0·041; 0·040; 0·039; 0·046. Length of gubernaculum: 0·023; 0·024; 0·022; 0·026. Length of tail: 0·143; 0·153; 0·148; 0·151. Cloacal diameter: 0·038; 0·047; 0·042; 0·041.

FEMALES: Body length: 2·34; 2·76. Body breadth: 0·073; 0·069. Head diameter: 0·023; 0·026. Length of cephalic setae: 0·006; 0·007. Oesophagus length: 0·42; 0·46. Length of tail: 0·257; 0·261. Anal diameter: 0·047; 0·049. Size of eggs: 0·053 × 0·042.

The structure of the head and of the cuticle is described on pages 171, 175 but it may be stressed that this species is easily recognized in collections by the extreme thickness of the cuticle over the oesophageal region of the body (Text-fig. 97).

The spicules are evenly curved, without proximal swellings or alae and terminate distally in sharp points. The lateral pieces of the gubernaculum are fairly broad and L-shaped. The short, distal arm of the gubernaculum carries a slight bulge on its inner surface which can be difficult to see on whole specimens but is immediately obvious on dissection. There is a median raised region of the cuticle anterior to the cloacal opening.

This species cannot be confused with any other because of the features diagnostic of the genus *Parapinnanema* (page 175). The discovery of further species referable to that genus must be awaited before a more restricted diagnosis can be established.

Graphonema georgei sp. nov.

(Text-figs. 80–84; 96; 99)

Weed and associated sand in hold-fasts on exposed rocks, Goode Beach, Albany W.A.

Measurements (mm.).

MALES. Body length: 1·30; 1·42. Body breadth: 0·052; 0·044. Diameter of head: 0·014; 0·014. Oesophagus length: 0·187; 0·198. Length of cephalic setae; intermediate/outer: 0·0026/0·0040; 0·0026/0·0040. Spicule length: 0·039; 0·043. Gubernaculum length: 0·017; 0·017. Tail length: 0·150; 0·164. Cloacal diameter: 0·036; 0·039.

The structure of the head is described above (page 180) and that of the cuticle on page 178. It may be stressed that the species is easily recognized by the swollen anterior end, the relatively posterior position of the amphids, the intermediate and the outer circles of setose cephalic sense organs, and the rather thin and delicate appearance of the cuticle.

The spicules are equal in length and identical in structure, fairly massive in appearance with narrow alae and slightly barbed posterior ends. The lateral pieces of the gubernaculum are relatively small and are a slightly curved L-shape (Text-fig. 96). The tail is long and slim and there is no pre-cloacal thickening on the mid-ventral surface of the body (Text-fig. 99).

The only other species referred to this genus is *G. vulgaris* Cobb, 1898 which is described without illustrations. All the cephalic setae are described as lying relatively near the anterior end of the body, while in the specimens from Western Australia they are far posterior to the same level. This difference could be because Cobb studied specimens in which the head was somewhat contracted but this appears unlikely as he refers to a number of papillae (eighteen) near the border of the mouth opening. These I interpret as the rugae which surround the mouth opening and the fact that they could be seen implies that the mouth was not fully closed.

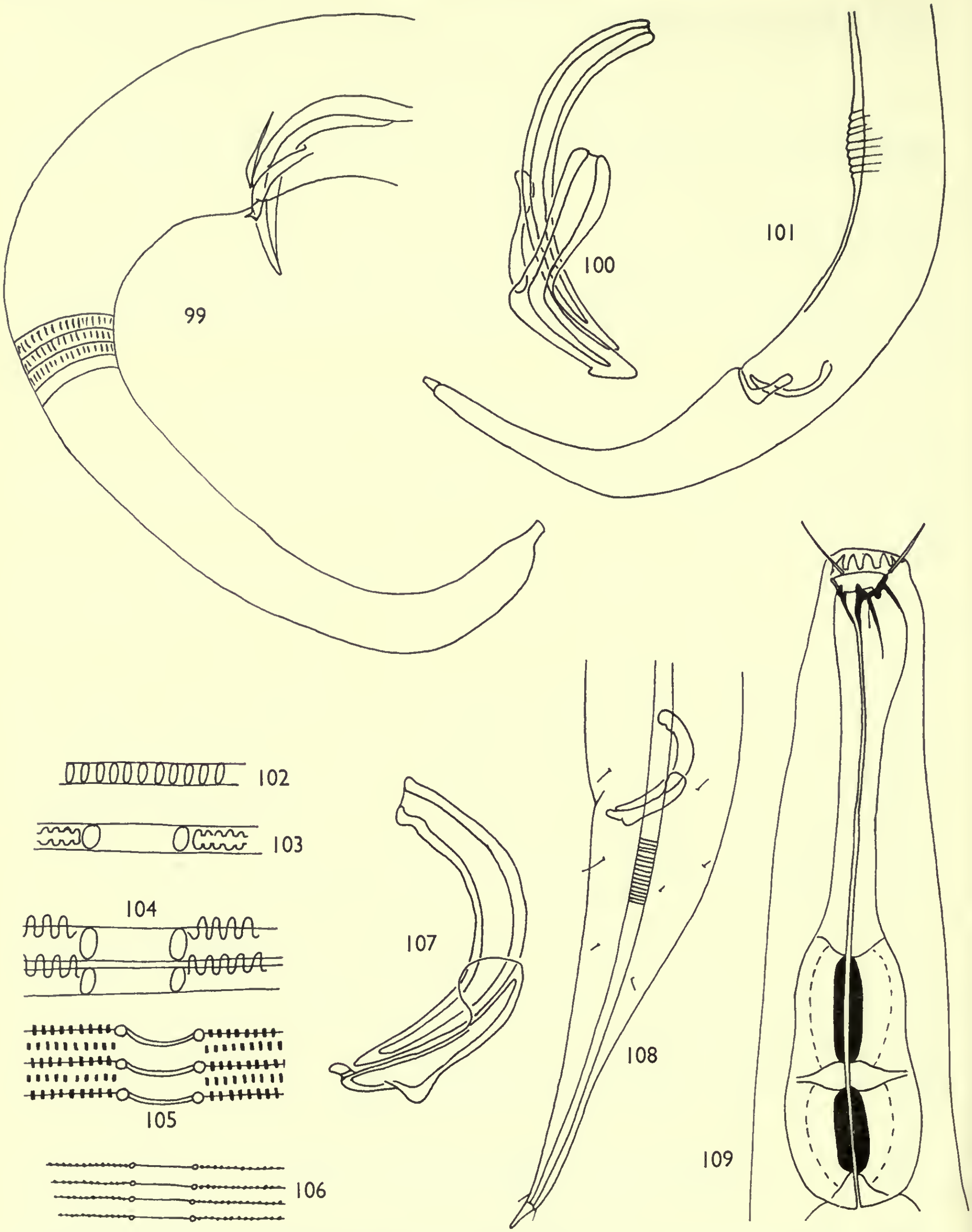
Cobb describes the spicules as " . . . of uniform size throughout, and are twice as long as the anal body diameter." while in the Western Australian specimens the spicules narrow markedly towards their extreme posterior ends and are about one cloacal width in length.

As a result of these differences I propose to treat the specimens from Western Australia as a distinct, new species, *G. georgei* sp. nov.

Austranema alii (Murphy, 1965) comb. nov.

(Text-figs. 38–40; 100–101)

Weed and sand from trawl from 12 metres in Shark Bay, W.A.; midway between Dirk Hartog Island and Denham.



FIGS. 99–109. 99. *Graphonema georgei.* Lateral view of male tail. 100–101. *Austranema alii.* 100. Gubernaculum and spicules. Fig. 101. Lateral view of male tail. 102–109. *Hypodontolaimus slacksmithi.* 102–106. Surface appearance of cuticle. 102. Between cephalic setae and anterior end of lateral differentiation. 103. Anterior end of lateral differentiation. 104. At anterior end of oesophageal bulb. 105. At posterior end of oesophagus. 106. At level of cloacal opening. 107. Gubernaculum and spicules. 108. Male tail. 109. Oesophagus.

Measurements (mm.).

Males. Body length: 1·70; 1·78; 2·16. Body breadth: 0·052; 0·046; 0·057. Head diameter: 0·016; 0·017; 0·019. Setae length: 0·005; 0·005; 0·005. Oesophagus length: 0·22; 0·24; 0·27. Spicule length: 0·044; 0·038; 0·052. Gubernaculun length: 0·026; 0·021; 0·035. Pre-cloacal supplement, length/distance anterior to cloacal opening: 0·048/0·098; 0·034/0·091; 0·047/0·130. Tail length: 0·19; 0·19; 0·22. Cloacal diameter: 0·038; 0·033; 0·049.

Females. Body length: 1·90; 2·31. Body breadth: 0·051; 0·057. Head diameter: 0·019; 0·021. Setae length: 0·004; 0·005. Oesophagus length: 0·27; 0·32. Tail length: 0·19; 0·21. Anal diameter: 0·033; 0·037. Vulva from anterior end: 0·90; 1·06. Size of eggs: 0·089 × 0·033; 0·074 × 0·036.

The spicules are equal and identical (Text-fig. 100). The lateral pieces of the gubernaculum are L-shaped with each arm about the same length. The distal end of the gubernaculum is slightly pointed and bears a slight notch on the under edge near the tip. There is a median pre-cloacal ventral modification in the form of a raised region of the cuticle. The three or four cuticular projections which ". . . appear to form a kind of bursa . . ." (Murphy, 1965, page 207) are due to the dense annules within the cuticle at the level of the cloacal opening projecting above the general body surface. This is because the cloacal opening itself is surrounded by an unannulate region and the projections represent the outer border of this region.

There are distinct granules lying on the lateral surface of the body between the annules, in a position corresponding to the lateral plates in *Euchromadora* species.

A. alii differs from the other species referred to the genus most particularly in the notched distal end to the lateral pieces of the gubernaculum and in the characteristic shape of the spicules.

Hypodontolaimus slacksmithi sp. nov.

(Text-figs. 56–59; 102–109)

Sand and weed brought up in trawl from 12 m.; Shark Bay, midway between Dirk Hartog Island and Denham, W.A. (Type locality).

Weed and hold-fasts on rocky flat in 12 cm. water; Cowaramup Bay, W.A.

Measurements (mm.).

Males. Body length: 1·34; 1·46. Body breadth: 0·051; 0·052. Length of cephalic setae: 0·020; 0·022. Diameter of head: 0·036; 0·038. Length of oesophagus: 0·19; 0·23. Length of spicules: 0·039; 0·044. Length of gubernaculum: 0·030; 0·031. Length of tail: 0·13; 0·15; Cloacal diameter: 0·033: 0·042.

Females. Body length: 1·38; 1·43. Body breadth: 0·075; 0·080. Length of cephalic setae: 0·021; 0·022. Diameter of head: 0·033; 0·037. Length of oesophagus: 0·22; 0·24. Distance of vulva from anterior end of body: 0·57; 0·63. Length of tail: 0·14; 0·17. Anal diameter: 0·039; 0·041.

The cuticular markings consist of prominent ovoid punctations just posterior to the cephalic setae (Text-fig. 102) and remain like this until the lateral differentiation begins about half-way along the oesophagus length. Here the lateral differentiation, which is raised above the general surface of the body, consists of a bar flanked by large dots in turn flanked by battlement-like punctations which occur on both sides of the annules (Text-fig. 103). By the level of the anterior end of the oesophageal bulb, the lateral markings have become wholly battlement-like along the anterior edge of each annule. At the posterior end of the oesophagus, the lateral bars of the differentiation are narrow, the large dots flanking them are relatively small and the markings outside these again are now in the form of small, squarish punctations of which one row is level with the large dots of the lateral differentiation while one row lies between the large dots (Text-figs. 104–105). The punctations continue to become simpler posteriorly and less prominent until by the level of the cloaca or anus they consist of rows of small dots while the lateral differentiation consists of a clear strip flanked by a series of punctations which are only very slightly larger than those found elsewhere on the surface of the body (Text-fig. 106). There appear to be four files of ventro- and dorso-lateral setae on the body but they are small and indistinct.

The mouth opening is bounded by twelve lobes, without rugae, which are supported by twelve flanges of the cheilorhabdion. These flanges project inwards and over the cavity of the cheilostome as rather hook-like structures in optical section. The cephalic sense organs consist of two circles of six papillae and an outer circle of four long setae. The amphid was not seen but the head is set-off from the body. The tail narrows fairly rapidly and ends in a long, pointed spinerette.

The oesophastome contains a very large, hollow dorsal onchium with a prominent dorsal apophysis in the male. The dorsal side of the oesophastome is very thick and slightly irregular in optical section longitudinally (Text-fig. 59). There is a lateral flange on each lateral wall of the retangular oesophastome, in *en face* view, which is highest towards the ventral side, and there is a single cone-like, anteriorly directed onchium on each ventro-lateral sector (Text-figs. 57–59).

The oesophagus ends posteriorly in a very prominent double bulb with a prominent cuticular lining (Text-fig. 109), of which the anterior bulb is slightly smaller than the more posterior.

The spicules are evenly curved and taper posteriorly to finely rounded ends. The gubernaculum is about two-thirds of the length of the spicules and is prominent with anterior, lateral processes which lie over the spicules laterally. There is a pair of slight bumps near the distal end of the gubernaculum on the side away from the spicules (Text-fig. 107).

This species is referable to the subgenus *Ptycholaimellus* Cobb, 1920 of the genus *Hypodontolaimus* de Man, 1888 as recognized by Gerlach (1955) and as followed by Wieser & Hopper (1967). It would probably be better to treat the group as a full genus, if it is to be recognized at all. There is little value in recognizing subgenera within free-living marine nematodes since they simply add another name to be considered.

Be that as it may, *H. slacksmithi* is, therefore, similar to *H. carinatus* Cobb, 1920; *H. poncticus* Filipjev, 1922; *H. pandispiculatus* Hopper, 1961 and *H. macrodentatus* Timm, 1961, from all of which it differs in the relatively stout, smoothly curved spicules and the massive gubernaculum.

SUMMARY OF GENERA AND SPECIES RECOGNIZED

Given here are brief summaries of the major diagnostic characters of the genera recognized and lists of the species referred to them. All genera are referred to the family Chromadoridae *sensu lato*.

EUCHROMADORA de Man, 1886

Head blunt with outer four sense organs setae; amphids without surrounding cuticular fringe; dorsal onchium solid; rows of denticles on lateral and ventral walls of oesophastome; oesophagus without posterior bulb; cuticle complex, unmarked dorsally and ventrally, not markedly thick over oesophageal region; lateral plates always present; no pre-cloacal modifications on male; tail short and stout.

Species:

E. vulgaris (Bastian, 1865); *E. gaulica* Inglis, 1962; *E. meadi* Wieser & Hopper, 1967; *E. permutabilis* Wieser, 1954; *E. tokiokai* Wieser, 1955; *E. striata* (Eberth, 1863); *E. eileenae* sp. nov.

STEINERIDORA gen. nov.

Generally similar to *Euchromadora*; differs in massive squarish dorsal onchium and sickle-like prominent onchia laterally and ventrally; oesophagus with posterior bulb; cuticular markings always about same size over full length of body laterally.

Species:

S. loricata (Steiner, 1916); *S. adriatica* (von Daday, 1901); *S. archaica* (Steiner & Hoeppli, 1926); *S.* (?) *dubia* (Steiner, 1918) sp. inq.

PARAPINNANEMA gen. nov.

Head set off as narrow region because of very thick cuticle over oesophagus length of body; intermediate circle of sense organs six setae and outer four setae; amphids with surrounding fringe of cuticle; dorsal onchium hollow; flanges on lateral walls and onchia ventrally in oesophastome; oesophagus without posterior bulb; cuticle very thick over oesophagus region and very battlement-like; cuticle with punctations dorsally and ventrally; tail long and slim; raised region of pre-cloacal modification on male.

Species:

P. wilsoni sp. nov.

PROTOCHROMADORA gen. nov.

Slim with rounded head; outer sense organs setae; dorsal onchium difficult to classify but frequently hollow looking; no elaborations on lateral walls of oesophastome but single onchium on each ventral sector; oesophagus without posterior bulb; amphid without cuticular fringe; cuticle not markedly thick over oesophageal region; cuticle complex (?) without punctations dorsally and ventrally; tail short and stout; no pre-cloacal modification.

Species:

P. scampae (Coles, 1965); *P. mediterranea* (Allgén, 1942); *P. parafricana* (Gerlach, 1958).

GRAPHONEMA Cobb, 1898

Head set off as swollen, bulb-like region; cephalic sense organs in three well separated circles, outer of four setae and intermediate of six setae; amphid relatively far posterior on head, with cuticular fringe; dorsal onchium small and hollow; lateral flanges and ventral onchia in oesophastome; oseophagus without posterior bulb; cuticle fairly thin with distinct annulations and punctations; tail long and slim; no pre-cloacal modification on male.

Species:

G. vulgaris Cobb, 1898; *G. georgei* sp. nov.; *G. amokurae* (Ditlevsen, 1921).

INNOCUONEMA gen. nov.

Dorsal onchium hollow; with associated dorsal swelling of oesophageal musculature; outer circle of cephalic sense organs setae; amphid not prominent; posterior oesophageal bulb present; cuticle complex; tail long and slim; no pre-cloacal modification on male.

Species:

I. flaccida (Wieser, 1959); *I. clovosa* (Wieser, 1959); *I. tentabunda* (de Man, 1890); *I. chilensis* nom. nov.

NYGMATONCHUS Cobb in Cobb, 1933

Cuticle complex anteriorly, elongate punctations posteriorly; lateral differentiation present; intermediate and outer circles of cephalic sense organs setae; dorsal onchium hollow; amphid with prominent double contour (?); no posterior oesophageal bulb; tail long and slim with pre-cloacal modification(?).

Species:

N. scriptus Cobb in Cobb, 1933; *N. fossiferus* Wieser, 1954; *N. bicornata* (Wieser, 1959) comb. nov.; *N. minutus* Gerlach, 1967.

AUSTRANEMA gen. nov.

Head not set off or blunt; dorsal onchium difficult to classify but generally hollow and anteriorly directed; outer and intermediate cephalic sense organs in one circle of ten setae; flanges laterally and onchia ventrally in oesophastome; oesophagus without posterior bulb, although expanded evenly posteriorly; cuticle complex, marked dorsally and ventrally, and thickened over oesophagus region; tail long and thin; pre-cloacal mid-ventral modification present on males.

Species:

A. colesi (Inglis, 1968); *A. shirleyae* (Coles, 1965); *A. alii* (Murphy, 1965); *A. pectinata* (Wieser & Hopper, 1967).

LIST OF NOMENCLATURAL CHANGES PROPOSED

Chromadora
paraheterophya Allgén, 1932 = *species dubia*
sabangensis Steiner, 1915 = *species inquirenda*
spectabilis Allgén, 1932 = *species dubia*
suilla Allgén, 1947 = *species dubia*
tentabunda de Man, 1890 = *Innocuonema t.* comb. nov.
Dicriconema
tenuis Steiner & Hoeppli, 1926 = *species inquirenda*

Euchromadora
archaica Steiner & Hoeppli, 1926 = *Steineridora a.* comb. nov.
arctica Filipjev, 1946 = *incertae sedis*
colesi Inglis, 1968 = *Austranema c.* comb. nov.
denticulata Cobb, 1914 = *species inquirenda*
dubia Steiner, 1915 = *Steineridora* (?) *d.* comb. nov.
hupferi Steiner, 1918 = *species dubia*
inflatispiculum Schuurmans Stekhoven, 1943 = *incertae sedis*
mediterranea Allgén, 1947 = *Protochromadora m.* comb. nov.
meridiana Cobb, 1914 = *species inquirenda*
parafricana Gerlach, 1958 = *Protochromadora p.* comb. nov.
pectinata Wieser & Hopper, 1967 = *Austranema p.* comb. nov.
scampae Coles, 1965 = *Protochromadora s.* comb. nov.
shirleyae Coles, 1965 = *Austranema s.* comb. nov.
stateni Allgén, 1930 = *species dubia*
Graphonema
amokuroides Wieser, 1954 = *Innocuonema chilensis* nom. nov.
clovosa Wieser, 1959 = *Innocuonema c.* comb. nov.
flaccida Wieser, 1959 = *Innocuonema f.* comb. nov.
Neochromadora
bicornata Wieser, 1959 = *Nygmatonchus b.* comb. nov.
Nygmatonchus
alii Murphy, 1965 = *Austranema a.* comb. nov.
Odontocricus
hupferi Steiner, 1918 = *species dubia*

Pareuchromadora
  fragilis Allgén, 1942 = *species dubia*
  setifer Schuurmans Stekhoven, 1943 = *species inquirenda*

Spilophora
  adriatica v. Daday, 1901 = *Steineridora a.* comb. nov.
  amokurae Ditlevsen, 1921 = *Steineridora a.* comb. nov.
  amokuroides Allgén, 1927 = *species dubia*
  loricata Steiner, 1916 = *Steineridora l.* comb. nov.
  norvegica Allgén, 1932 = *species dubia*
  pusilla Allgén, 1947 = *species dubia*

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Hypodontolaimus slacksmithi is named in appreciation of Mr. Slack-Smith's efforts on my behalf; *Euchromadora eileenae* is a small token of appreciation for Miss Mitchell's endurance in sorting formalin samples while *Austranema wilsoni* and *Graphonema georgei* are named in honour of Dr. B. R. Wilson and Dr. R. W. George respectively, W.A. Museum for the many kindnesses shown to me by them and their families during my stay in Perth, W.A.

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J. S. RYLAND

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1. INTRODUCTION

Hincks' great work "A History of the British Marine Polyzoa" was published in 1880. Some measure of its status can be gauged from a comparison of both text and plates with those of Johnston's "British Zoophytes" (1847). Benefiting from the works of Gray (1848), Busk (1852, 1854, 1859, 1875) and Smitt (1865–72), as well as from shorter contributions by himself and other naturalists, Hincks produced a monograph in which the species were taxonomically well ordered, accurately and unmistakably described, and illustrated with clarity and fidelity. The result was a book which had a much greater significance than just that of a descriptive catalogue for identifying British marine Polyzoa.

Hincks maintained some large, unwieldy and now clearly unnatural genera (e.g. *Membranipora* s. lat., *Lepralia*, *Cellepora*). Later taxonomists, such as Norman (1903), Levinsen (1909) and Canu & Bassler (in a wide range of publications) have split these large assemblages into smaller, more homogeneous units. The importance of Hincks' book lies in the fact that so many of today's genera and their types have been based on his descriptions and plates.

In addition to being a source-book to workers on Polyzoa all over the world, it remains the most comprehensive text for biologists wishing to identify marine Polyzoa in western Europe. (A key to the genera was subsequently provided by

Harmer, 1896 : 525.) The general user of the book today is handicapped by Hincks' nomenclature, now frequently obsolete. New genera have been introduced; specific names have changed through the operation of the Law of Priority, through " splitting ", or because Hincks had wrongly synonymized the species he was describing. His " varieties ", in particular, constitute a hazard. Some are varieties in a modern (though not genetically defined) sense, others simply growth forms; some represent fossils unknown from Recent seas, others have never been found in Britain—such particulars are often not clearly stated. Many of the " varieties " are now recognized as specifically distinct: such is often the case with his " deep-water " forms, where one name conceals two ecologically complementary species, whose proper discrimination is important. All this affects not only the name, but also the geographical distribution of the taxa, and Hincks' statements of distribution beyond the British Isles are quite unreliable.

Finally, a fauna is not static: immigrant species, as well as a few then overlooked, have increased the number found around the British Islands. The British collections (his own and those of various contemporaries, particularly Norman and Jelly) on which Hincks worked, were gathered from the seas immediately surrounding the British Isles. Within these limits Hincks' work is remarkably complete. Very few forms have been found that are not at least recognizably mentioned in the book. For the present list the larger area shown on the map (Text-fig. 4) has been covered, as explained on p. 237. Except for the Entoprocta, the long list of additional species consists largely of records from localities outside Hincks' range, and is not to be seen as a list of his omissions.

Many users of the " British Marine Polyzoa ", having made an identification, want to know the currently valid name. This need has determined the arrangement of this paper. The presentation shows, on the left, the page number and then the name used by Hincks. Then follows the name I accept, with author and date. Where explanatory notes are required, these follow; they include a reference to any closely similar species subsequently discovered around Britain. Species not included by Hincks are listed separately (p. 235).

Merely to present the specific name used by Hincks, together with its modern equivalent, would be unsatisfactory for several reasons. Sometimes, for a proper identification to be made, Hincks' descriptions must be supplemented, and in such cases appropriate references have been given. Occasionally there is lack of unanimity among workers as to what the " right " name is: where possible I have stated my own views. In a majority of cases the name listed is the one in current use, but I have provided the essential documentation concerning the adoption of that name. Obviously I have not been able to assess the merits of every name given; some names therefore represent the considered opinion of other workers. Nevertheless, there are many cases in which new or rediscovered information about generic and specific names and their authorship is included.

Finally, this list is intended as a working document, not as a final judgment. I hope it will assist users of the " British Marine Polyzoa " to obtain the maximum value from the book, and serve as a signpost to some of the remaining nomenclatural problems, and that it may prepare the way for a formal checklist.

The main part of the index originates from a set of record cards maintained for some years at the British Museum (Natural History) by Dr. Anna B. Hastings, and the idea of a compilation of this kind is hers. As, however, I had the time and facilities to prepare the index for publication, I undertook to do so. During this process the paper ceased to be a list and became the documented account which follows. Throughout the work I have been encouraged by Dr. Hastings, who also placed at my disposal a number of unpublished manuscripts, references to which have been given as appropriate. It gives me great pleasure to thank Dr. Hastings both for making available these important sources of information and for her continued interest throughout the preparatory period. Some of the work has been carried out at the British Museum (Natural History); Miss Patricia L. Cook has here always given me every assistance, and I wish to thank her for this valuable help.

2. INDEX TO THE "BRITISH MARINE POLYZOA"

CHEILOSTOMATA

4 *Aetea anguina*, Linnaeus: ***Aetea anguina*** (Linnaeus, 1758).

Type-species by monotypy of *Aetea* Lamouroux (1812 : 184).

6 *A. recta*, Hincks: ***Aetea sica*** (Couch, 1844).

There are no valid grounds for rejecting the name introduced by Couch (1844 : 102)—see Marcus (1955 : 278, 314)—despite Hincks' (1880*a* : 7, footnote) objection to it.

8 *A. truncata*, Landsborough: ***Aetea truncata*** (Landsborough, 1852).

14 *Eucratea chelata*, Linnaeus: ***Scruparia chelata*** (Linnaeus, 1758) and ***Scruparia ambigua*** (d'Orbigny, 1841).

Eucratea chelata as described by Hincks comprises two species, which have been separated and defined by Hastings (1941). 294 *Hippothoa cassiterides* (see p. 224) is also referred to *S. ambigua*.

Scruparia chelata (*Sertularia chelata* Linnaeus, 1758) was selected by Harmer (1923 : 316) as type-species of *Scruparia* Oken (1815). Oken's *Lehrbuch* (1815) was later rejected for nomenclatural purposes by the International Commission on Zoological Nomenclature (1956). Application for the validation of *Scruparia* has subsequently been made to the International Commission by Ryland (1967*a*).

Var α *repens*. Probably ***S. ambigua*** (d'Orbigny), see Hastings (1941).

Var. β *gracilis*: ***S. ambigua*** (d'Orbigny), see Hastings (1941).

18 *Gemellaria loricata*, Linnaeus: ***Eucratea loricata*** (Linnaeus, 1758).

Type-species of *Eucratea* Lamouroux (1812 : 183), selected by Harmer (1923 : 307).

24 *Scruparia clavata*, Hincks: ***Haplota clavata*** (Hincks, 1857).

Type-species by monotypy of *Haplota* Marcus (1940 : 208), discussed by Marcus (1950 : 13).

27 *Huxleya fragilis*, Dyster: ***Huxleya fragilis*** Dyster, 1858.

Type-species by monotypy of *Huxleya* Dyster (1858 : 260).

28 *Brettia pellucida*, Dyster: ***Brettia pellucida*** Dyster, 1858.

Type-species by monotypy of *Brettia* Dyster (1858 : 260).

29 *B. tubaeformis*: ***Bicellariella ciliata*** (Linnaeus, 1758).

Brettia tubaeformis, described by Hincks (1879 : 154), is based on the ancestrular parts of *Bicellariella ciliata* (see 68), here illustrated in Text-fig. 1.

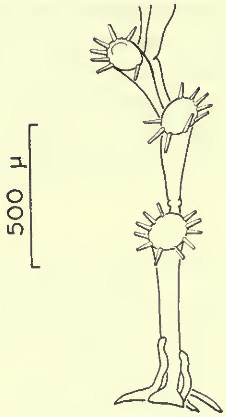

FIG. 1. Ancestrula and first zooids of *Bicellariella ciliata* (L.), Skomer, West Wales, 50 ft., June 1966.

34 *Cellularia Peachii*, Busk: ***Tricellaria peachii*** (Busk, 1851).

Type-species by original designation of *Bugulopsis* Verrill (1879 : 29; 1880 : 190), a genus maintained by Kluge (1962 : 367) and Prenant & Bobin (1966 : 441). Like Marcus (1940 : 162), however, I am following Harmer (1923 : 355), who included *Bugulopsis* in *Tricellaria*, commenting that *T. peachii* " appears to represent the extreme amount of loss of structures which typically occur in the genus, as shown by the disappearance of the frontal and marginal avicularia and of the scutum ". Species showing comparable simplification in structure occur, for example, in *Bugula*.

38 *Menipea ternata*, Ellis and Solander: ***Tricellaria ternata*** (Ellis & Solander, 1786).

Type-species by monotypy of *Tricellaria* Fleming (1828 : 540).

42 *M. Jeffreysii*, Norman: ***Notoplites jeffreysii*** (Norman, 1868).

Hincks' figure of this species (Pl. IX, fig. 1), which is seriously inaccurate, has been reproduced by both Kluge (1962 : 370, fig. 231) and Prenant & Bobin (1966 : 445, fig. 147, I). Norman (1893 : 446) redescribed the species, and Ryland (1963*b* : 17, fig. 4) provided a new illustration.

Referred to *Notoplites* gen. n. by Harmer (1923 : 351).

45 *Scrupocellaria scruposa*, Linnaeus: ***Scrupocellaria scruposa*** (Linnaeus, 1758).

Type-species by monotypy of *Scrupocellaria* van Beneden (1845*b* : 26).

46 *S. elliptica*, Reuss: ***Scrupocellaria inermis*** Norman, 1867.

Norman (1893 : 451, footnote) showed that Hincks wrongly synonymized

S. inermis Norman (1867) with the fossil species *S. elliptica*. *S. inermis* Waters (1897 : 8) is a different species (Ryland, 1963*b* : 12).

48 *S. scabra*, Van Beneden: ***Scrupocellaria scabra*** (van Beneden, 1848).

50 *S. scrupea*, Busk: ***Scrupocellaria scrupea*** Busk, 1851.

52 *S. reptans*, Linnaeus: ***Scrupocellaria reptans*** (Linnaeus, 1758).

59 *Caberea Ellisii*, Fleming: ***Caberea ellisii*** (Fleming, 1814).

61 *C. Boryi*, Audouin: ***Caberea boryi*** (Audouin, 1826).

68 *Bicellaria ciliata*, Linnaeus: ***Bicellariella ciliata*** (Linnaeus, 1758).

See also 29 *Brettia tubaeformis* and Text-fig. 1. Type-species by monotypy of *Bicellariella* Levinsen (1909 : 431, pro *Bicellaria* de Blainville, preoccupied).

70 *B. Alderi*, Busk: ***Bicellarina alderi*** (Busk, 1860).

Type-species by monotypy of *Bicellarina* Levinsen (1909 : 99).

75 *Bugula avicularia*, Linnaeus: ***Bugula avicularia*** (Linnaeus, 1758).

Bugula was introduced by Oken (1815), in a work which was rejected for nomenclatural purposes by the International Commission in 1956. Application for validation of *Bugula* has been made to the International Commission by Ryland (1967*a*).

Compare *B. stolonifera* (p. 240).

77 *B. turbinata*, Alder: ***Bugula turbinata*** Alder, 1857.

80 *B. flabellata*, J. V. Thompson: ***Bugula flabellata*** (Thompson in Gray, 1848).

Compare *B. fulva* (p. 240).

82 *B. calathus*, Norman: ***Bugula calathus*** Norman, 1868.

84 *B. plumosa*, Pallas: ***Bugula plumosa*** (Pallas, 1766).

See discussion under 89 *B. purpurotincta*.

86 *B. gracilis*, Busk, var. *uncinata*, Hincks. Considered by Ryland (1960) to be based on *Bugula turrita* (Desor), and not British.

89 *B. purpurotincta*, Norman: ***Bugula purpurotincta*** Norman, 1868.

Kluge (1962 : 342) and Prenant & Bobin (1966 : 519) have incorrectly applied the name *fastigiata* to this species. They claim that *Cellularia fastigiata* Dalyell (1847 : 236) represents a valid introduction: but this is not the case, for Dalyell identified his species as *Sertularia fastigiata* Linnaeus (1758 : 815). Reference to Linnaeus shows that *S. fastigiata* was based on the Soft-feathered Coralline of Ellis (1755 : 33, pl. 18)—see discussion in Harmer (1930 : 81–84) on Linnaeus' use of Ellis' work. The Soft-feathered Coralline is indubitably the species currently known as *Bugula plumosa* (Pallas)—see 84—so that, by the Law of Priority, *B. fastigiata* must be the correct name for that species. However, to replace such a well-known name as *plumosa* would not be sensible, especially in view of the recent application of the Linnaean name to *B. purpurotincta*.

Likewise, the use of *fastigiata* by Alder (1856 : 149), in the binomen *Bugula fastigiata*, does not represent a valid introduction, since Alder identified his species as *Sertularia fastigiata*. The introduction of *purpurotincta*, in combination with *Bugula*, by Norman (1868 : 219) is valid.

Application for the suppression of *Sertularia fastigiata* has been made to the International Commission (Ryland, 1968*c*).

92 *B. Murrayana*, Johnston: **Dendrobeania murrayana** (Bean in Johnston, 1847).

Type-species by monotypy of *Dendrobeania* Levinsen (1909 : 99, 113).

Var. α (*fruticosa*, Packard): **Dendrobeania fruticosa** (Packard, 1863). See p. 240. According to Kluge (1962 : 330), however, the form illustrated by Hincks belongs to *D. pseudomurrayana* Kluge, 1955, var. *fessa* Kluge, 1955.

96 *Beania mirabilis*, Johnston: **Beania mirabilis** Johnston, 1840.

Type-species by monotypy of *Beania* Johnston (1840).

100 *Notamia bursaria*, Linnaeus: **Epistomia bursaria** (Linnaeus, 1758).

Type-species by original designation of *Epistomia* Fleming (1828 : 541).

106 *Cellaria fistulosa*, Linnaeus.

The complex nomenclatural tangle involving the three species of *Cellaria* has been referred to the International Commission on Zoological Nomenclature (Ryland, 1968*a*).

109 *C. sinuosa*, Hassall (see above).

112 *C. Johnsoni*, Busk (see above).

115 *Flustra foliacea*, Linnaeus: **Flustra foliacea** (Linnaeus, 1758).

Type-species of *Flustra* Linnaeus (1761), see Lang (1917).

118 *F. papyracea*, Ellis and Solander: **Chartella papyracea** (Ellis & Solander, 1786).

Type-species of *Chartella* Gray (1848), not by monotypy as stated by Harmer (1923), but now considered as selected by him.

The conclusions of Hastings (MS) on the status of the genus *Chartella*, which I have accepted, differ from those of Silén (1941 : 49–56) and Prenant & Bobin (1966 : 183) who follow him. Silén merged *Chartella* with *Carbasea* (see 123), but Hastings regards it as a valid genus. Among characters distinguishing the two genera, the nature of the brood-chamber is particularly important. *Chartella* has endozooidal ovicells closed by a special membranous operculum; *Carbasea* has either internal ovisacs or endozooidal ovicells closed by the zooidal operculum (Hastings, MS on *Chartella*).

120 *F. securifrons*, Pallas: **Securiflustra securifrons** (Pallas, 1766).

Type-species by original designation of *Securiflustra* Silén (1941).

Var. (*papyracea*, Dalyell). This species displays a number of variations in colony form. One of these, in which the fronds were wider than usual, was illustrated by Dalyell (1848 : 22, Pl. VII) as *Flustra papyracea* ? Hincks listed this as a variety, without renaming it, though it hardly deserves varietal status (Hastings, MS on *Securiflustra*). This name should not be confused with *Chartella papyracea* (Ellis & Solander).

122 *F. Barleei*, Busk: **Chartella barleei** (Busk, 1860).

Type-species by original designation of *Terminoflustra* Silén (1941) which, however, Hastings places in the synonymy of *Chartella* Gray. The presence of avicularia hardly seems a character of sufficient importance to warrant generic separation of species currently classified as *Terminoflustra* from *Chartella* (cf. *Bugula neritina* and other species of that genus). The resemblance is otherwise close, particularly in the form and method of closure of the ovicells (Hastings, MS on *Chartella*).

123 *F. carbasea*, Ellis and Solander: ***Carbasea carbasea*** (Ellis & Solander, 1786).

Type-species by abolute tautonymy of *Carbasea* Gray (1848), see Harmer (1923 : 301).

129 *Membranipora Lacroixii*, Audouin: ***Conopeum reticulum*** (Linnaeus, 1767).

Type-species by monotypy of *Conopeum* Gray (1848 : 108, 146). The Linnaean name has priority over that of Audouin (see Harmer, 1926 : 210); in any case it seems unlikely that *Membranipora lacroixii* Busk (1854 : 60 pars) and Hincks (1880*a* : 129) belong to Audouin's species (Levinsen, 1909 : 144).

Compare also *C. seurati* (p. 238).

131 *M. monostachys*, Busk: ***Electra monostachys*** (Busk, 1854).

E. monostachys is without question the valid name for this species, often at present (e.g. by Marcus, 1940 : 118; Prenant & Bobin, 1966 : 150) called *E. hastingsae* Marcus. Busk (1854 : 61) based his account on two species, both still present in his collection, but only one was illustrated (Pl. LXX, 1–4), and figure 3 at least is based on a specimen in the British Museum (1899. 7.1.1089). Hincks (1880*a*) used this, together with additional material, when preparing his account of *M. monostachys*. Marcus (1937 : 39; 1950 : 7), believing that all Busk's material belonged to *Electra crustulenta* (Pallas), introduced *E. hastingsae* for what he thought to be *E. monostachys* Hincks non Busk. As they are the same, Marcus' name is a junior synonym (Hastings, MS on brackish-water membraniporine Polyzoa).

Var. α (*fossaria*): ***Electra crustulenta*** (Pallas, 1766). Borg (1931) elucidated the synonymy of *Electra crustulenta*, including in that species *Membranipora monostachys* var. *fossaria* Hincks. Borg recognized var. *fossaria*, together with a number of other varieties of *E. crustulenta* which he considered to be morphologically and ecologically or geographically distinct; if valid, these would today be regarded as subspecies. One of them, at least, represents a distinct species (var. *spiculata*, which is *Conopeum seurati*, see p. 238). Zeeland is the type-locality for *E. crustulenta*, and Britain is the type-locality of var. *fossaria*, so, if Borg was right in identifying his material from Holland with the latter, the name *fossaria* can have no subspecific validity. British *E. crustulenta* shows variation, but it is not yet clear whether varieties are distinguishable or whether the varieties *fossaria*, *typica* and *baltica* recognized by Borg (1931) will prove to be distinct. A full revision, based on plentiful material, is needed (Hastings, MS on brackish-water membraniporine Polyzoa).

134 *M. catenularia*, Jameson: ***Pyripora catenularia*** (Fleming, 1828).

This species should be attributed to Fleming, see Thomas & Larwood (1956).

137 *M. pilosa*, Linnaeus: ***Electra pilosa*** (Linnaeus, 1761).

The type-species of *Electra* Lamouroux (1816) is *Flustra verticillata* Ellis & Solander (1786), which has generally been considered as a junior synonym of *E. pilosa*—a view recently challenged by Bobin & Prenant (1960) and Prenant & Bobin (1966 : 136).

Electra Gray (1866) [Mammalia] is a junior homonym.

Var. α (*dentata*): var. **dentata** Ellis & Solander, 1786.

Var. β (*laxa*, Smitt): var. **laxa** Smitt, 1868.

Var. γ [Pallas, in text]: var. **ellisina** Moll, 1803. This variety (a growth form of the colony), which has also been named var. *flustriformis* (Norman, 1894 : 120) is referred by Prenant & Bobin (1966 : 146) to var. *ellisina* Moll (1803 : 41), which was based on the Irregular spongy foliaceous Coralline of Ellis (1755 : 73, pl. 29 D, 31).

Norman (1894) described many varieties of *E. pilosa* (see also Prenant & Bobin, 1966 : 145).

140 *M. membranacea*, Linnaeus: ***Membranipora membranacea*** (Linnaeus, 1767).
Type-species of *Membranipora* de Blainville (1830 : 447), see Borg (1931 : 5).

143 *M. hexagona*, Busk.
Based on damaged zooids of some other species (Hastings, 1966 : 66); not *M. hexagona* (v. Hagenow, 1839) in Voigt (1959) and Berthelsen (1962).

143 *M. lineata*, Linnaeus: ***Callopora lineata*** (Linnaeus, 1767).
Type-species by monotypy of *Callopora* Gray (1848).
Var. α (in text): a minor variant.

147 *M. craticula*, Alder: ***Callopora craticula*** (Alder, 1856).
Referred to *Callopora* by Norman (1903*a* : 589).

149 *M. spinifera*, Johnston: ***Cauloramphus spiniferum*** (Johnston, 1832).
Type-species by original designation of *Cauloramphus* Norman (1903*a* : 587).

151 *M. flustroides*, Hincks: ***Hincksina flustroides*** (Hincks, 1877).
Type-species by original designation of *Hincksina* Norman (1903*a* : 585).

152 *M. discreta*, Hincks: ***Callopora discreta*** (Hincks, 1862).
Referred to *Callopora* by Osburn (1923 : 7).

153 *M. curvirostris*, Hincks: ***Parellisina curvirostris*** (Hincks, 1862).
Type-species by original designation of *Parellisina* Osburn (1940).

154 *M. unicornis*, Fleming: ***Tegella unicornis*** (Fleming, 1828).
Type-species of *Tegella* Levinsen (1909 : 152) designated by Canu & Bassler (1920).

156 *M. Dumerilii*, Audouin: ***Callopora dumerilii*** (Audouin, 1826).
Referred to *Callopora* by Norman (1903*a* : 589).

158 *M. solidula*, Alder and Hincks: ***Alderina solidula*** (Hincks, 1860).
Referred to *Alderina*, with reservations, by Norman (1903*a* : 596).

159 *M. aurita*, Hincks: ***Callopora aurita*** (Hincks, 1877).
Referred to *Callopora* by Norman (1903*a* : 589).

160 *M. imbellis*, Hincks: ***Alderina imbellis*** (Hincks, 1860).
Type-species by original designation of *Alderina* Norman (1903*a* : 596).

162 *M. Flemingii*, Busk: ***Amphiblestrum flemingii*** (Busk, 1854).
Gray (1848) introduced *Amphiblestrum* monotypical for *Flustra membranacea* Müller, which is generally accepted as a synonym of *Electra crustulenta* (Pallas) not of *Membranipora membranacea* (Linn.), see Borg (1931 : 2, 10). Gray listed a number of specimens referred to Müller's species by Johnston. The latter's account (1847 : 328) was evidently based on more than one species, one of which was *Electra crustulenta*. Gray's brief definition (p. 146) is applicable, as far as

it goes, to *E. crustulenta*, but not to the other species. Of the Johnston specimens remaining in the British Museum, none belongs to *E. crustulenta*. They comprise three somewhat similar species which had not been distinguished from each other when Gray was writing (*Tegella unicornis*, *Callopora aurita* and *Amphiblestrum flemingii* in this list). Busk (1854 : 58) examined this material and introduced the name *Membranipora flemingii*, based on more than one species. It remained for Hincks (1880) satisfactorily to discriminate the species involved, so giving an unambiguous definition of *M. flemingii* (Hastings, MS on the collections of George Busk and George Johnston).

Busk (1854) did not at first adopt the genus *Amphiblestrum*. When he did so (1884 : 65) he took *M. flemingii* as the type-species. This selection was accepted by Norman (1903*a* : 586, 596), and by most subsequent authors. While final acceptance of *M. flemingii* as type-species must depend on its recognition by the International Commission, it would, in our view, be detrimental to nomenclatural stability to accept Borg's (1931 : 29) view that the type-species of *Amphiblestrum* should be *Flustra membranacea* Müller. *Amphiblestrum* would then become a subjective junior synonym of *Electra* Lamouroux.

164 *M. cornigera*, Busk: ***Larnacicus corniger*** (Busk, 1860).

Type-species by original designation of *Larnacicus* Norman (1903*b* : 87).

166 *M. Rosselii*, Audouin: ***Rosseliana rosselii*** (Audouin, 1826) and
R. rosselii var. ***multijuncta*** (Waters, 1879).

Flustra Rosselii Audouin (1826) is type-species by original designation of *Rosseliana* Jullien (1888 : 78). *Membranipora Rosselii* in Hincks comprises two taxa: *Rosseliana rosselii* and its variety *multijuncta* (Waters, 1879 : 120, Pl. XIII, fig. 4, as *Diachoris patellaria* var. *multijuncta*) (Hastings, MS on *Rosseliana* and *Mollia*). This variety is referred to as *Rosseliana* "sp. nov." by Gautier (1962 : 63–64). Hincks' illustration (Pl. XXII, fig. 4) probably represents *R. rosselii* s. str., but the zooids depicted are not very typical. *R. rosselii* and its variety may be distinguished as follows (Hastings, MS):

> Cryptocyst of majority of zooids not occupying more than half the length of aperture, its transverse border straight or concave and without opesiular indentations; connecting tubes not visible **R. rosselii**
>
> Cryptocyst occupying more than half the length of the aperture, its border somewhat convex, often with a trace of opesiular indentations; connecting tubes usually visible in at least part of the colony var. ***multijuncta***

167 *M. trifolium*, S. Wood: ***Amphiblestrum solidum*** (Packard, 1863).

According to Lagaaij (1952 : 26), the North Atlantic species described by Hincks under this name is not the same as Wood's (1844) species and should be called *Amphiblestrum solidum* (Packard, 1863).

Var. α (*quadrata*): var. ***quadrata*** Hincks, 1880.

169 *M. minax*, Busk: ***Amphiblestrum minax*** (Busk, 1860).

Type-species by original designation of *Ramphonotus* Norman (1894), which does not, however, in the opinion of Hastings and myself, differ sufficiently in any significant way from *Amphiblestrum* Gray to warrant its separate maintenance.

In his Introduction, Hincks (1880*a* : lxxiii) distinguished as *M. princeps* sp. n. the form illustrated by Smitt (1868*a*, Pl. 20, fig. 44), in which the avicularium is larger than usual. Norman (1903*a*) argued that this form merely shows the avicularia in a more developed state, a conclusion accepted by subsequent writers.

170 *M. nodulosa*, Hincks: ***Ammatophora nodulosa*** (Hincks, 1877).

Type-species by original designation of *Ammatophora* Norman (1903*b* : 88).

172 *Megapora ringens*, Busk: ***Megapora ringens*** (Busk, 1856).

Type-species by original designation of *Megapora* Hincks (1877*c*).

174 *Micropora coriacea*, Esper: ***Micropora coriacea*** (Johnston, 1847) and ***Micropora normani*** Levinsen, 1909.

Hincks' account includes two species (Hastings, 1966), *M. coriacea* (Johnston), non Esper (1806–?, Pl. 7), type-species by monotypy of *Micropora* Gray (1848), see Harmer (1926) and Brown (1952), and *M. normani* Levinsen (1909 : 162).

Flustra coriacea Esper (1806–?) is a synonym of *Cellepora* (now *Calpensia*) *nobilis* Esper (1796 : 145). So is *Eschara impressa* Moll (1803), recorded from the Channel Islands by Norman (1907) as *Micropora impressa* (see p. 239). *Membranipora calpensis* Busk (1854), type-species by original designation of *Calpensia* Jullien (1888 : 78), which has generally been considered as a further synonym of *Calpensia nobilis* (Esper), has been shown by Buge (1957 : 173) to be a distinct species.

175 *M. complanata*, Norman.

The taxonomic placing of *Lepralia complanata* Norman (1864) is uncertain, and has been discussed by Gautier (1962 : 67). It is not a *Micropora*, but an ascophoran: as a temporary measure it can still be called *Lepralia*, which, in the opinion of Harmer (1957 : 1101) has no type-species and " . . . should remain available for the numerous species referred by authors to that genus, at present not placed in other genera ". See also Harmer (1897 : 52).

178 *Steganoporella Smittii*: ***Thalamoporella rozieri*** (Audouin, 1826).

Placed by Harmer (1926) in the synonymy of *Flustra rozieri* Audouin, type-species by original designation of *Thalamoporella* Hincks (1887 : 164).

181 *Setosella vulnerata*, Busk: ***Setosella vulnerata*** (Busk, 1860).

Type-species by original designation of *Setosella* Hincks (1877*c*).

185 *Cribrilina radiata*, Moll: ***Cribrilaria radiata*** (Moll, 1803).

Type-species by original designation of *Cribrilaria* Canu & Bassler (1929 : 33). Placed by Harmer (1926 : 475) and many subsequent authors including Prenant & Bobin (1966 : 589) in *Colletosia* Jullien (1886). But the type-species of *Colletosia* is *Lepralia endlicheri* Reuss (1848), now known to be referable to *Umbonula* Hincks—see entry 317—(Bobies, 1956; Brown, 1958).

Form i [*radiata*]: ***Cribrilaria radiata*** (Moll, 1803).

Form ii [*innominata*]: var. ***innominata*** Couch, 1844.

The status of the "*innominata* form" (*Lepralia innominata* Couch, 1844 : 114) has been much argued, often with the result of its again receiving the status of species. I have followed Osburn (1950 : 187) in treating it as a variety, but note that Prenant & Bobin (1966 : 589) comment: "Nous avons la conviction personelle que ces deux espèces sont indépendantes", so that the matter is far from settled.

Var. α: ***Puellina setosa*** (Waters, 1899).

Var. β. Friedl (1917) gave the name *Cribrilina radiata* var. *hincksi* to a variety described by Hincks (1880*b* : 74, Pl. X, fig. 7). Prenant & Bobin (1966 : 595) follow Canu & Bassler (1930 : 30) in giving the variety specific rank, and include among their illustrations a copy of the present var. β (1880*a*, Pl. XXV, fig. 4). In my opinion, however, var. β and *C. hincksi* are not the same.

Var. γ (*tenuirostris*). Not British.

190 *C. punctata*, Hassall: ***Cribrilina punctata*** (Hassall, 1841) and
C. cryptooecium Norman, 1903.

C. punctata is type-species by monotypy of *Cribrilina* Gray (1848).

Norman (1903*b* : 102) considered that Hincks had included two species under his *C. punctata*, and referred Pl. XXIV, fig. 3 and Pl. XXVI, fig. 3, to *C. cryptooecium* sp. n. Although not mentioned by Marcus (1940), *C. cryptooecium* is accepted by Kluge (1962 : 393) and Prenant & Bobin (1966 : 580).

Var. α. Norman (1903) considered this a variety of *C. punctata* s. str.

Recent examination of the type-specimen of *C. punctata* has revealed that it also belongs to *C. cryptooecium*. To avoid disrupting the established nomenclature, application has been made to the International Commission on Zoological Nomenclature (Ryland & Stebbing, 1968) to set aside the present lectotype (Lagaaij, 1952 : 56) and to designate a neotype such that the name *C. punctata* retains its accepted identity.

193 *C. annulata*, Fabricius: ***Cribrilina annulata*** (Fabricius, 1780).

196 *C. figularis*, Johnston: ***Figularia figularis*** (Johnston, 1847).

Type-species by original designation of *Figularia* Jullien (1886).

Var. α (*fissa*): ***Figularia fissa*** (Hincks, 1880). Harmer (1926 : 479) raised this variety to specific rank. It is not British.

198 *C. Gattyae*, Busk: ***Puellina gattyae*** (Landsborough, 1852).

Type-species by monotypy of *Puellina* Jullien (1886). *Lepralia gattyae* was not introduced by Busk (1854 : 73) but by Landsborough (1852 : 326), though the name may have been suggested by Busk.

Var. α. No information.

200 *Membraniporella nitida*, Johnston: ***Membraniporella nitida*** (Johnston, 1838).

Type-species of *Membraniporella* Smitt (1873 : 10) designated by Hincks (1877*c* : 526). Compare *Callopora rylandi* (p. 239), which is superficially similar in appearance.

202 *M. melolontha*, Busk: ***Aspidelectra melolontha*** (Landsborough, 1852).

Type-species by monotypy of *Aspidelectra* Levinsen (1909). As Hastings (1966 : 63) has noted, *Lepralia melolontha* was introduced by Landsborough (1852 : 319) and not by Busk (1854 : 78).

206 *Microporella ciliata*, Pallas: ***Microporella ciliata*** (Pallas, 1766).

Type-species by original designation of *Microporella* Hincks (1877*c* : 526). Application was made by Brown (1955) to place the genus *Microporella* and the species *ciliata* on the Official Lists of Names in Zoology (see also 244 *Schizoporella vulgaris*).

Var. *personata*: ***M. ciliata*** (Pallas), **personate form** (Harmer, 1957 : 961).

Californian variety: ***M. cribrosa*** Osburn, 1952. Not British.

Australian variety: ***M. orientalis*** Harmer, 1957. Not British.

211 *M. Malusii*, Audouin: ***Fenestrulina malusii*** (Audouin, 1826).

Type-species by original designation of *Fenestrulina* Jullien (1888 : 37).

While I follow all recent authors in referring *M. malusii* to *Fenestrulina* Jullien, it should be noted that the genus has not yet been satisfactorily defined in a way that makes clear how it differs from *Microporella* s. str. (cf. Levinsen, 1909 : 329).

Var. α (*thyreophora*): var. ***thyreophora*** Busk, 1857. Not British.

Var. β (*vitrea*). No information.

Another variety, not mentioned in the text, was illustrated by Hincks in Pl. XXIX, fig. 12.

214 *M. impressa*, Audouin: ***Haplopoma graniferum*** (Johnston, 1847).

Lagaaij (1952 : 61) and Ryland (1963*a* : 16) have shown that *Microporella impressa* Hincks (excluding the varieties) non Audouin, is the species described by Johnston (1847 : 309) as *Lepralia granifera*. *Haplopoma impressum* Marcus (1940 : 216) non Audouin is *H. planum* Ryland (1963*a* : 14), see p. 241.

Var. α (? *bimucronata*, Moll : var. *cornuta*, Busk): ***Haplopoma bimucronatum*** (Moll, 1803). This variety is the *Eschara bimucronata* of Moll (1803), but not the var. *cornuta* of Busk (1854 : 83) which is probably, as described, a variety of *H. graniferum* (Johnston).

Var. β (*glabra*): ***Haplopoma impressum*** (Audouin, 1826). This variety (*Haplopoma impressum* var. *glabra* in Marcus, 1940 : 216) is true *Flustra impressa* Audouin (1826), see Lagaaij (1952 : 62) and Ryland (1963*a* : 11), type-species by monotypy of *Haplopoma* Levinsen (1909 : 280).

Var. γ (*pyriformis*, Busk): ***Haplopomella pyriformis*** (Busk, 1859). Placed by Buge (1953) in *Haplopomella* gen. n., of which it is type-species. Fossil only.

216 *M. violacea*, Johnston: ***Reptadeonella violacea*** (Johnston, 1847).

Type-species of *Reptadeonella* Busk (1884 : 180). The validity of *Reptadeonella*, for encrusting Adeonidae, has often been questioned, and its continued use appears to be largely a matter of convenience. It was maintained by Harmer (1957 : 814), whom I have followed.

Var. α: ***Reptadeonella insidiosa*** (Jullien, 1903). *Adeonella insidiosa* was introduced by Jullien (1903 : 54) for this variety. Compare, however, the view of Levinsen (1909 : 284).

Var. β (*plagiopora*): ***Reptadeonella plagiopora*** (Busk, 1859). Not British.

220 *Diporula verrucosa*, Peach: ***Diporula verrucosa*** (Peach, 1868).
Type-species by original designation of *Diporula* Hincks (1879 : 156).

224 *Chorizopora Brongniartii*, Audouin: ***Chorizopora brongniartii*** (Audouin, 1826).
Type-species by original designation of *Chorizopora* Hincks (1879).

229 *Porina borealis*, Busk: ***Tessaradoma boreale*** (Busk, 1860).
Type-species by monotypy of *Tessaradoma* Norman (1869). The non-availability of the specific name *gracile* M. Sars (1851), used by Marcus (1940), was discussed by Harmer (1957 : 852).

230 *Porina tubulosa*, Norman: ***Cylindroporella tubulosa*** (Norman, 1869).
Type-species by original designation of *Cylindroporella* Hincks (1877*c*).

233 *Anarthropora monodon*, Busk: ***Anarthropora monodon*** (Busk, 1860).
Type-species of *Anarthropora* Smitt (1868*b*), designated by Norman (1869).

235 *Lagenipora socialis*, Hincks: ***Lagenipora lepralioides*** (Norman, 1868).
L. socialis is the type-species by monotypy of *Lagenipora* Hincks (1877*b* : 214). Norman (1903*b* : 108) recognized that *L. socialis* was the same as *Celleporella lepralioides* Norman (1868), included separately by Hincks (1880*a* : 414). *Celleporella* as used by Norman was not the same genus as *Celleporella* Gray (1848), see Harmer (1957 : 822).

238 *Schizoporella unicornis*, Johnston: ***Schizoporella unicornis*** (Johnston in Wood, 1844).
Type-species by original designation of *Schizoporella* Hincks (1877*c*).
Form *ansata*: ***Schizoporella dunkeri*** (Reuss, 1848). The " deep-water form " of Hincks is not *Lepralia ansata* Johnston (1847), but *L. Dunkeri* Reuss (1848), described and discussed by Ryland (1968*b*). (See also *Schizoporella magnifica* Hincks and *S. longirostris* Hincks, p. 241.)

241 *S. spinifera*, Johnston: ***Escharina spinifera*** (Johnston, 1847).
Referred to *Escharina* Milne Edwards (1836) by Levinsen (1909).

243 *S. Alderi*, Busk: ***Escharina alderi*** (Busk, 1856).
Referred to *Escharina* by Levinsen (1909). Norman (1907) has distinguished a number of growth forms.

244 *S. vulgaris*, Moll: ***Escharina vulgaris*** (Moll, 1803).
Type-species by original designation of *Escharina* Milne Edwards (1836 : 218, also 230–231). Application to place the genus *Escharina* and the species *vulgaris* on the Official Lists of Names in Zoology was made by Brown (1955).

246 *S. simplex*, Johnston: ***Escharina johnstoni*** (Quelch, 1884).
Referred to *Escharina* by Levinsen (1909 : 326) but, whether as *Schizoporella* or *Escharina*, *simplex* Johnston (1847 : 305) is preoccupied by *simplex* d'Orbigny (1841). Quelch (1884 : 217) accordingly introduced a new name for the present species.

247 *S. linearis*, Hassall: ***Schizomavella linearis*** (Hassall, 1841).
Var. α (*hastata*, Hincks): ***Schizomavella hastata*** (Hincks, 1862). Gautier (1962 : 139) argued in favour of restoring this form to the rank of species, noting that the orifice and operculum are different from those of *S. linearis*.

Var. *β* (*mamillata*): var. ***mamillata*** Hincks, 1880. Treated as a species by Gautier (1958), but later (1962 : 143) as a variety. Not British but Mediterranean.

Var. *γ* (*nitida*): var. ***nitida*** Hincks, 1880. Not British but Mediterranean.

Var. *δ* (*crucifera*, Norman): var. ***crucifera*** Norman, 1869.

252 *S. sanguinea*, Norman: ***Schizobrachiella sanguinea*** (Norman, 1868).

Type-species by original designation of *Schizobrachiella* Canu & Bassler (1920 : 353).

254 *S. cristata*, Hincks: ***Schizomavella cristata*** (Hincks, 1879).

Probably referable to *Schizomavella*.

255 *S. biaperta*, Michelin: ***Buffonellaria divergens*** (Smitt, 1873).

The situation regarding this species, known in current literature as *Stephanosella biaperta* (Michelin), is extremely confused. *Eschara biaperta* was described by Michelin (1848 : 330, Pl. 79, fig. 3) from what is now termed the Savignéen facies of the Helvétian (Upper Miocene) at Doué-la-Fontaine (Maine-et-Loire), France (Buge, 1957). It is the type-species by original designation of *Stephanosella* Canu & Bassler (1917 : 40). The present confusion stems from the lack of precision in Michelin's description and a figure too small to show detail. Moreover, there is no type-specimen. Through the kindness of Dr. Émil Buge, I have been able to examine specimens from the Savignéen of Channay and Savigné-sur-Lathan (Indre-et-Loire), some 50 km. from Doué-la-Fontaine. Thus, though not exact topotypes, they are from a nearby exposure of the same facies; and they agree perfectly with Michelin's figure.

The encrusting convex zooids have a finely porous frontal wall, and a semicircular orifice provided with a narrow sinus (Text-fig. 2a). A prominent avicularian chamber is frequently present to one side of the orifice, and the mandible appears to be short and triangular with a rounded apex. The zooids have the appearance of an *Escharina* or *Schizoporella*, but, in the absence of ovicells, the question of generic relationship cannot be pursued. Busk (1859 : 47, Pl. 7, fig. 5) recorded *Lepralia biaperta* (?) from the English Coralline Crag (Pliocene), but his species was clearly different from the Savignéen specimens I have examined.

Smitt (1868*b* : 14, 98, Pl. 24, figs. 70–73), probably misled by Busk's figure, appears to have been the first author to apply Michelin's name to a Recent species. Smitt's *Escharella biaperta* is a species now well-known in Arctic regions, and further descriptions of it have been given by Nordgaard (1906 : 15, Pl. 1, figs. 12–14), Osburn (1952 : 368, Pl. 42, figs. 1–2), and Kluge (1962 : 477, fig. 370). There is very close agreement between the accounts of these four authors. The frontal wall is a smooth holocyst with marginal pores, and the orifice is elliptical with a shallow sinus and rounded condyles (Text-fig. 2b). Thus this species differs both in the form of the frontal wall and in the shape of the orifice from the Savignéen fossil.

In his account of polyzoa from Florida, Smitt (1873) again reported Michelin's species, this time using the combination *Hippothoa biaperta* (p. 46, Pl. 8, figs.

173–176). *H. biaperta* is clearly based on more than one species. In the same paper he introduced *H. divergens* (p. 47, Pl. 9, figs. 177 and 179). Hincks (1880*a* : 255) regarded these two species as identical, and most subsequent authors have accepted his opinion. Canu & Bassler (1927 : 8), however, created the genus *Buffonellaria* for *H. divergens* (form *typica*, Smitt's fig. 179).

The species described by Hincks (1880*a* : 255, Pl. XL, figs. 7–9), as *Schizoporella biaperta*, is identical with Smitt's *H. divergens*. Hincks recognized this, but treated *divergens* as a variety of *biaperta*. All British specimens were then referred to this variety. It differs from the Arctic species referred to above by having a very much deeper sinus to the orifice (Text-fig. 2c). I have examined a number of specimens in the British Museum, from Britain, France, Spain and Madeira, and find that the deep sinus is a constant character.

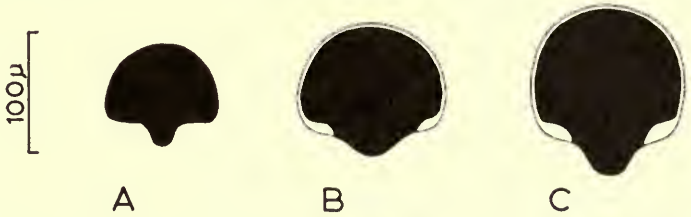

FIG. 2. Shape of the orifice in *Stephanosella biaperta* auctt. A.—*S. biaperta* (Michelin), Savignéen of Channay, France (specimen from the Institut de Paléontologie, Paris, lent by É. Buge); B.—*Buffonellaria* sp., Spitzbergen (Brit. Mus. 1862.3.13.49); C.—*B. divergens* (Smitt), Hastings, England (Brit. Mus. 1897.5.1.726).

Osburn (1952 : 320, 368) maintained that Hincks had confused *S. biaperta* (sensu Osburn) with another species, distinguished by having a tremocystal front wall, which he identified as *Schizoporella cornuta* (Gabb & Horn). It appears to me that this may be true only through Hincks' citation in synonymy of Smitt's *Hippothoa biaperta*. Curiously, Osburn does not mention Smitt's (1873) paper in his discussion of *S. cornuta*. Whether or not Smitt's *H. biaperta* is partly based on *S. cornuta*, the British species described by Hincks certainly is not.

Gautier (1962 : 155) appears to be correct in his assertion that the ovicellate specimen from Algeria (Brit. Mus. 1899.5.1.995), illustrated by Hincks in Pl. XL, fig. 9. represents another species—unnamed, but congeneric with the British material.

The following conclusions may be drawn from the foregoing discussion:

(a) The Recent species collectively known as *Stephanosella biaperta* (Michelin) are different specifically and generically from the Savignéen fossil which properly bears that name;

(b) The species found in southern Britain and southwards into warmer latitudes is conspecific with *Hippothoa divergens* Smitt, from Florida. It differs from a related Arctic species in the form of the orifice (Text-fig. 2b, c);

(c) *Hippothoa divergens* is type-species of *Buffonellaria*, and should be called *Buffonellaria divergens* (Smitt);

(d) The Arctic species called *Stephanosella biaperta* in current literature is congeneric with *B. divergens*, but specifically different and apparently unnamed;

(e) Hincks' Algerian specimen belongs to another species of *Buffonellaria*;

(f) *Schizoporella cornuta* is not a European species, but may have been included by Smitt (1873) in his Floridan *Hippothoa biaperta*.

258 *Schizoporella armata*, Hincks: ***Schizotheca armata*** (Hincks, 1862).

Levinsen (1909 : 294) allied this species to *Schizotheca* and *Rhynchozoon*, and the former appears to be the more appropriate.

260 *S. auriculata*, Hassall: ***Schizomavella auriculata*** (Hassall, 1842).

Type-species by original designation of *Schizomavella* Canu & Bassler (1917).

Var. *α ochracea* (= *Lepralia auriculata*, var. *Leontiniensis*, Waters [1878]): var. ***ochracea*** Hincks, 1862.

Var. *β* (*cuspidata*): ***Schizomavella umbonata*** (Busk, 1860)—see next entry.

264 *S. umbonata*, Busk: ***Schizomavella umbonata*** (Busk, 1860).

I have been unable to locate any type material of this species. There is, however, a slide in the British Museum (Natural History), 1963.2.12.155, labelled "*S. auriculata* v. *umbonata*. Guernsey" by Miss E. C. Jelly. This specimen has recently been relabelled as *S. auriculata* var. *cuspidata* Hincks. Following up this clue, both Dr. Anna B. Hastings and I have examined the Museum's specimens of var. *cuspidata*. In general appearance, zooids of *S. umbonata* and *S. auriculata* var. *cuspidata*, as depicted in Hincks' illustrations (Pl. XXIV, fig. 2, after Busk, and Pl. XXIX, fig. 8, respectively), are rather similar. The only major difference lies in the apparent presence of areolae in *S. umbonata*. Examination has shown that the frontal wall in var. *cuspidata* is a pleurocyst. The secondary thickening is granular, sometimes incorporating a small number of non-peripheral pores. The final appearance of the wall varies somewhat from colony to colony, but in 1963.2.12.155 the thickening forms distinct centripetally-directed ridges originating between the marginal pores, and reminiscent of the effect depicted by Busk (1860*b* : 143, Pl. 27, fig. 1) in his illustration. We believe that it is justifiable to place *S. auriculata* var. *cuspidata* Hincks, 1880, in the synonymy of *S. umbonata*.

The orifice of *S. umbonata*, despite some variation in the shape of the sinus, differs clearly from that of *S. auriculata* (Text-fig. 3).

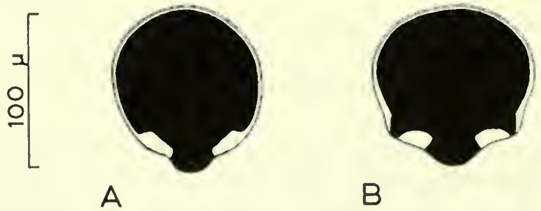

FIG. 3. A.—Orifice of *Schizomavella auriculata* (Hassall), Raasay Sound, Scotland (author's specimen); B.—Orifice of *S. umbonata* (Busk), unknown British locality (Brit. Mus. 1911.10.1.1558).

As just mentioned, the frontal wall of *S. umbonata* is a porous pleurocyst; in *S. auriculata*, on the other hand, it is a tremocyst. *S. umbonata* is thus specifically distinct from *S. auriculata*; indeed, following presently accepted taxonomic practice, the difference between the two is sufficient to warrant placing *S. umbonata* in a different genus (*S. auriculata* is type-species of *Schizomavella*). There is however, at the present time, no alternative genus available; and in any case, the full implications of regarding the mode of secondary thickening as invariably constituting a generic character have yet to be assessed. The remaining characters of *S. umbonata* suggest affinity with *S. auriculata*.

265 *S. discoidea*, Busk: ***Schizomavella discoidea*** (Busk, 1859).

Referred to *Schizomavella* by Gautier (1962); the description has been amplified by Ryland (1963*c* : 17).

266 *S. sinuosa*, Busk: ***Stomachetosella sinuosa*** (Busk, 1860).

Referred to *Stomachetosella* Canu & Bassler (1917) by O'Donoghue & O'Donoghue (1926).

Var. *armata*: var. ***armata*** Hincks, 1880. Not British; no additional information.

269 *S. Cecilii*, Audouin: ***Arthropoma cecilii*** (Audouin, 1826).

Type-species of *Arthropoma* Levinsen (1909 : 332), selected by Canu & Bassler (1920 : 351).

270 *S. cruenta*, Norman: ***Stomachetosella cruenta*** (Busk, 1854).

Referred to *Stomachetosella* by Osburn (1952 : 306). The name was introduced by Busk (1854 : 69).

271 *S. hyalina*, Linnaeus: ***Celleporella hyalina*** (Linnaeus, 1767).

Type-species by monotypy of *Celleporella* Gray (1848), but considered by Waters (1900) as referable to *Hippothoa*. The form of the colony (uniserial or coherent crust) does not provide a clear and valid distinction between *Hippothoa* and *Celleporella*, but they may prove to be distinguished by the types of polymorphic individuals present or by the nature of the interzooidal communications. Further study is needed. (Hastings, MS on *Hippothoa*.)

Var. α (*cornuta*): This is ***Hippothoa cornuta*** Busk, 1854, var. ***aporosa*** Levinsen, 1909. Not British.

Var. β (*incrassata*): var. ***incrassata*** Hincks, 1880.

Var. γ (*tuberculata*): var. ***tuberculata*** Hincks, 1880. Not British; but not *Hippothoa hyalina* var. *tuberculata* Brown (1952).

The status of these three varieties and var. *tuberculata* Brown, together with a fourth variety that Hincks defined and figured (p. 274; Pl. XLV, fig. 3) but did not name, is being considered by Hastings (MS on *Hippothoa*).

276 *S. venusta*, Norman: ***Trypostega venusta*** (Norman, 1864).

Type-species by monotypy of *Trypostega* Levinsen (1909).

279 *Mastigophora Dutertrei*, Audouin: ***Escharina dutertrei*** (Audouin, 1826).

Referred to *Escharina* by Levinsen (1909).

Form α: ***Escharina dutertrei*** (Audouin).

Form β. No information.

281 *M. Hyndmanni,* Johnston: **Escharina hyndmanni** (Johnston, 1847).

Type-species of *Herentia* Gray (1848) selected by Brown (1952) who, however, considered the genus to be synonymous with *Escharina.* Buge (1957 : 234) distinguished *Herentia* from *Escharina* chiefly on account of the interzooidal position of the vibracula. But Hastings (1963*b* : 168) showed that the vibracula are also of this kind in *E. vulgaris,* type-species of *Escharina.*

Var. *ensiformis* (in text) is not British.

Var. *porosa* (in text) is not British.

284 *Schizotheca fissa,* Busk: **Schizotheca fissa** (Busk, 1856).

Type-species by original designation of *Schizotheca* Hincks (1877*c*).

285 *S. divisa,* Norman: **Schizotheca divisa** (Norman, 1864).

288 *Hippothoa divaricata,* Lamouroux: **Hippothoa divaricata** Lamouroux, 1821.

Type-species by monotypy of *Hippothoa* Lamouroux (1821 : 82).

Var. α (*conferta*): var. **conferta** Hincks, 1880.

Var. β (*carinata,* Norman): var. **carinata** Norman, 1875.

Var. γ (*Patagonica,* Busk): **Hippothoa patagonica** Busk, 1852. A valid species (Hastings, MS on *Hippothoa*). Not British.

291 *H. expansa,* Dawson: **Hippothoa expansa** Dawson, 1859. (See addendum.)

293 *H. flagellum,* Manzoni: **Hippothoa distans** P. H. MacGillivray, 1869.

Hippothoa flagellum Manzoni (1870*b*) is a junior synonym of *H. distans* MacGillivray (1869) (synonymy given by Harmer, 1957 : 951). The confusion which arose in Gautier's (1962 : 119) account will be explained by Hastings (MS on *Hippothoa*).

294 [*H. cassiterides,* Couch]: On the basis of Fig. 87 in Johnston (1847 : 477), this is fairly clearly *Scruparia ambigua* (d'Orbigny)—see 14 *Eucratea chelata.*

297 *Lepralia Pallasiana,* Moll: **Cryptosula pallasiana** (Moll, 1803).

Type-species by original designation of *Cryptosula* Canu & Bassler (1925).

299 *L. canthariformis,* Busk.

Introduced by Busk (1860*b* : 143), but there is no further information, and no specimens are available.

300 *L. foliacea,* Ellis and Solander: **Pentapora foliacea** (Ellis & Solander, 1786).

Type-species of *Pentapora* Fischer (1807 : 307), designated by Hastings & Ryland (1968).

Var α (*fascialis*): **Pentapora fascialis** (Pallas, 1766). Opinion has been divided as to the status of *Eschara fascialis* Pallas (1766 : 43). I have accepted the most recent view, that of Gautier (1962 : 165). In any case, it would not seem nomenclaturally permissible to regard *fascialis* (1766) as a variety of *foliacea* (1786).

Var. β (*bidentata,* M.-Edwards). This is based on the appearance of the older ovicellate zooids (Hastings & Ryland, 1968): it is not a variety.

305 *L. pertusa,* Esper: **Hippoporina pertusa** (Esper, 1796).

Referred to *Hippodiplosia* Canu (1916) by Marcus (1940 : 251) and others; but is, in fact, the type-species of *Hippoporina* Neviani (1895: 109), designated by Waters (1918 : 98), see discussion in Hastings & Ryland (1968).

307 *L. adpressa,* Busk: **Hippopodinella lata** (Busk, 1856).

Not *L. adpressa* Busk (1854 : 82), see Lagaaij (1952 : 129), but *L. lata* Busk (1856 : 309).

Var. α: **Hippopodinella adpressa** (Busk, 1854). This is *L. adpressa* Busk (1854), type-species by original designation of *Hippopodinella* Barroso (1924), and not British.

309 *L. hippopus,* Smitt: **Hippoporella hippopus** (Smitt, 1867).

Type-species by monotypy of *Hippoporella* Canu (1917).

311 *L. edax,* Busk: **Hippoporidra edax** (Busk, 1859).

Type-species by original designation of *Hippoporidra* Canu & Bassler (1927).

315 *L. polita,* Norman: **Hemicyclopora polita** (Norman, 1864).

Type-species by original designation of *Hemicyclopora* Norman (1894). *L. discrepans* Jullien (1903 : 72) appears to be a synonym.

317 *Umbonella* [replaced on p. cxxxviii and in Vol. II by *Umbonula*] *verrucosa,* Esper: **Umbonula littoralis** Hastings (1944) and
Umbonula ovicellata Hastings (1944).

U. verrucosa is type-species by monotypy of *Umbonula* Hincks (1880). Hincks included two different species under this heading (regarding them merely as shallow and deep-water forms), which have been described subsequently as *Umbonula littoralis* Hastings (1944) and *U. ovicellata* Hastings (1944), illustrated by Hincks in Pl. XXXIX, figs. 1 and 2 respectively. The latter, which alone extends into the Mediterranean (Gautier, 1962), is evidently, as Hastings suggested, identical with Esper's species. Since the name *Cellepora verrucosa* Esper (1790) is a junior homonym of *C. verrucosa* Linnaeus (1767), it is invalid and not available for the type-species of the genus, which is, therefore, *Umbonula ovicellata* Hastings.

323 *Porella concinna,* Busk: **Porella concinna** (Busk, 1854).

Var. α (*Belli,* Dawson): **Porella concinna** var. **belli** Dawson, 1859. *Lepralia Belli* Dawson (1859 : 256) has been the source of considerable confusion in the past, but Kluge's recent opinion (1962 : 432) is to agree with Hincks in regarding it as a variety of *P. concinna.*

Var. β (*gracilis*): **Smittina bella** (Busk, 1860). This " variety " is *Smittina bella* (see Norman, 1894; and Osburn 1952 : 403), which Hincks described on p. 352.

326 *P. minuta,* Norman: **Porella minuta** (Norman, 1869).

329 *P. struma,* Norman: **Porella struma** (Norman, 1868).

330 *P. compressa,* Sowerby: **Porella compressa** (Sowerby, 1805).

It is frequently assumed, e.g. by Bassler (1953) and Harmer (1957), that this species is type of the genus *Porella.* However, if Lagaaij's discussion (1952 : 97) is read in conjunction with Art. 70 of the International Rules, it seems that *Millepora cervicornis* Pallas (1766) should be taken as the species intended by Gray (1848).

In view of Osburn's (1952 : 391) clear indication that *Millepora compressa* Sowerby (non Linnaeus, 1758) and *M. cervicornis* are not congeneric, the type-species must be fixed by application to the International Commission (Ryland 1968*d*).

334 *P. Laevis*, Fleming: ***Porella laevis*** (Fleming, 1828).

336 *Escharoides rosacea*, Busk: ***Ragionula rosacea*** (Busk, 1856).

Generic placing is confused on both nomenclatural and systematic grounds. Verrill (in Kumlien, 1879 : 149; also Verrill, 1880 : 196) proposed *Escharopsis* for " two Northern Atlantic species *E. lobata* (Lamx. [1821 : 40]) = *E. Sarsi* Smitt [1868*b* : 24–25], and *E. rosacea*, both common in the Gulf of St. Lawrence ". The type-species was designated by Norman (1903 : 123) as " *Escharopsis lobata*, Lamouroux, = *E. Sarsii*, Smitt ". The doubt expressed by Smitt (1868) as to whether his *Escharoides Sarsii* was truly *Eschara lobata* Lamouroux has persisted. At least, there is nothing in Lamouroux' diagnosis contrary to the view of their being conspecific, nor in the provenance of his specimen " Sur le *Fucus nodosus*, aux environs du banc de Terre-Neuve ". The provisions of Art. 70 of the International Rules apply to both Verrill's and Norman's papers, so that Lamouroux' name should be accepted. Thus it is not true that *Escharopsis* is an invalid genus (Osburn, 1952; Bassler, 1953; but cf. Kluge, 1962), but the type should be called *Escharopsis lobata* (Lamouroux, 1821) and not *E. sarsii* (Smitt, 1868) as in Kluge (1962).

Kluge places *Escharoides rosacea* in the same genus, as *Escharopsis rosacea* (Busk, 1856), and there is nothing nomenclaturally against this. Osburn (1952 : 310) remarks, however, that this species was formerly assigned to various genera (including *Escharopsis*) " until Canu and Bassler [1927] very properly erected a new genus for it ". In Osburn's view, which I have provisionally accepted, the species is *Ragionula rosacea*, type-species by original designation of *Ragionula* Canu & Bassler (1927 : 7).

339 *E. quincuncialis*, Norman.

This species is now generally referred to *Leiosella* Canu & Bassler (1917 : 48) (Canu & Bassler, 1925; Gautier, 1962) as *L. quincuncialis* (Norman, 1867). In my opinion, however, the generic position of this species requires further consideration.

341 *Smittia Landsborovii*, Johnston: ***Smittina landsborovii*** (Johnston, 1847).

Type-species by original designation of *Smittina* Norman (1903*b* : 120) (pro *Smittia* Hincks 1879, preoccupied).

Form α (*crystallina*, Norman): var. ***crystallina*** Norman, 1867.

Form β (? *porifera*, Smitt). *Escharella porifera* Smitt (1868*b* : 9) f. *typica*, which was not indicated by Hincks (in synonymy), is referred to as *Schizomavella porifera* (Smitt, 1868) by Osburn (1952 : 332); f. *minuscula* is referred to as *Smittina minuscula* (Smitt, 1868) by Kluge (1962 : 426); f. *majuscula* is referred to *Smittina arctica* (Norman, 1894) by Osburn (1952 : 402), but as *Smittina majuscula* (Smitt, 1868) by Kluge (1962 : 425), which appears to be nomenclaturally correct. However, all three species are Arctic, and most unlikely to have been found by Hincks (1880*a* : 345) off the south coast of Devon.

346 *S. reticulata*, J. Macgillivray: ***Smittoidea reticulata*** (J. Macgillivray, 1842).

Referred to *Smittoidea* gen. n. by Osburn (1952 : 409).

348 *S. affinis*, Hincks: ***Smittina affinis*** (Hincks, 1862).

This species, introduced by Hincks (1862 : 206), does not appear to conform to the diagnoses of any of the genera formerly regarded as comprising *Smittina* s. lat. as defined by (Osburn, 1952). The difference lies solely in the orientation of the avicularium, otherwise it is closely similar to species of *Smittina* s. str. The definition of this genus must evidently include a statement that the avicularium may be longitudinally or transversely orientated, or wanting (as in *S. cheilostoma*).

349 *S. cheilostoma*, Manzoni: ***Smittina cheilostoma*** (Manzoni, 1870).

350 *S. marmorea*, Hincks: ***Smittoidea marmorea*** (Hincks, 1877).

Referred to *Smittoidea* gen. n. by Osburn (1952).

352 *S. bella*, Busk: ***Smittina bella*** (Busk, 1860).

See also under 323 *Porella concinna.*

353 *S. trispinosa*, Johnston: ***Parasmittina trispinosa*** (Johnston, 1838).

Referred to *Parasmittina* gen. n. by Osburn (1952).

Var. α (*Jeffreysi*, Norman): ***Parasmittina jeffreysi*** (Norman, 1876) [in Jeffreys, 1876 : 208]. Type-species by original designation of *Parasmittina* Osburn (1952).

357 *Phylactella labrosa*, Busk: ***Phylactella labrosa*** (Busk, 1854).

Type-species of *Phylactella* Hincks (1879) designated by Canu & Bassler (1917). Bassler (1953) renamed *P. labrosa* Hincks (1880*a*) as *Phylactellipora hincksi*, on the fallacious assumption that *P. labrosa* Hincks was different from *P. labrosa* Busk (see Ryland, 1963*b*).

Osburn's (1952) account of this genus is extremely confused, and his designation of *Lepralia collaris* Norman (see below) as type-species is invalid. *Phylactella* Hincks is a junior objective synonym of *Alysidota* Busk (1856), type-species *Lepralia labrosa* Busk (1856) by original designation, but which is preoccupied by *Alysidota* Agassiz (1846). *Alysidotella* Strand (1928), proposed specifically to replace *Alysidota* Busk non Agassiz, is therefore a junior objective synonym of *Phylactella* Hincks.

358 *P. collaris*, Norman: ***Phylactellipora collaris*** (Norman, 1867).

Type-species by original designation of *Phylactellipora* Bassler (1953 : 217), who, however, reversed the diagnoses of *Phylactella* and *Phylactellipora* (Ryland, 1963*b* : 29).

359 *P. eximia*, Hincks: ***Phylactella eximia*** (Hincks, 1860).

360 *Mucronella Peachii*, Johnston: ***Escharella immersa*** (Fleming, 1828).

Type-species of *Escharella* Gray (1848) selected by Norman (1903*b* : 117). For a discussion of the priority and validity of both *Escharella* and *immersa* Fleming, see Ryland (1963*b* : 18).

Var. α (*labiosa*, Busk): var. ***labiosa*** Busk, 1856.

Var. β (*octodentata*): ***Escharella octodentata*** (Hincks, 1880). For discussion of status, see Ryland (1963*b* : 24).

363 *M. ventricosa*, Hassall: ***Escharella ventricosa*** (Hassall, 1842).

See also p. 242.

366 *M. variolosa*, Johnston: ***Escharella variolosa*** (Johnston, 1838).

368 *M. laqueata*, Norman: ***Escharella laqueata*** (Norman, 1864).

369 *M. abyssicola*, Norman: ***Escharella abyssicola*** (Norman, 1869).

370 *M. microstoma*, Norman: ***Hemicyclopora microstoma*** (Norman, 1864).
Referred by Ryland (1963*b* : 27, footnote) to *Hemicyclopora* Norman (1894), so *Escharella microstoma* in Kluge (1962) cannot be the same species.

371 *M. coccinea*: ***Escharoides coccineus*** (Abildgaard, 1806).
Type-species of *Escharoides* Milne Edwards (1836 : 218, 259) subsequently designated by Verrill in Kumlien (1879 : 149).
Var. α (*mamillata*): ***Escharoides mamillata*** (Wood, 1844). Considered a species by Lagaaij (1952) and Ryland (1963*c*).

376 *M. pavonella*, Alder: ***Umbonula arctica*** (M. Sars, 1851).
Referred to *Umbonula* Hincks by Harmer (1902 : 296). *Lepralia arctica* Sars takes priority over *Eschara pavonella* Alder, 1864.

378 *Palmicellaria elegans*, Alder: ***Palmicellaria elegans*** Alder, 1864.
Type-species by monotypy of *Palmicellaria* Alder (1864).

379 *P. Skenei*, Ellis and Solander: ***Palmicellaria skenei*** (Ellis & Solander, 1786).
Var. α (*bicornis*): var. ***bicornis*** Busk, 1859. Varietal status discussed by Ryland (1963*c*).
Var. β (*foliacea*): var. ***foliacea*** Hincks, 1880.
Var. *tridens* (in text): var. ***tridens*** Busk, 1856. Not British.

382 *P. lorea*, Alder: ***Palmicellaria lorea*** (Alder, 1864). No additional information.

384 *P.* (?) *cribraria*, Johnston: ***Palmicellaria cribraria*** (Johnston, 1847).
No additional information.

385 *Rhynchopora bispinosa*, Johnston: ***Rhynchozoon bispinosum*** (Johnston, 1847).
Type-species of *Rhynchozoon* Hincks, 1895 (Index, p. v) pro *Rhynchopora* Hincks, 1877*b* (preoccupied by *Rhynchopora* King [Brachiopoda]), of which it was type-species by original designation.

391 *Retepora Beaniana*, King: ***Sertella beaniana*** (King, 1846).
Type-species of *Sertella* Jullien (1903) selected by Canu & Bassler (1920). For additional species of *Sertella* see p. 242.

395 *R. Couchii*, Hincks: ***Sertella couchii*** (Hincks, 1878).
Referred to *Sertella* by Jullien (1903).

398 *Cellepora pumicosa*, Linnaeus: ***Celleporaria pumicosa*** (Pallas, 1766).
Hincks was incorrect in attributing this species to Linnaeus (1767), and has caused subsequent confusion by doing so. *Millepora pumicosa* was introduced by Pallas (1766 : 254), and his first reference was to Ray and the second to the Porous Eschara of Ellis (1755 : 75, Pl. 27 F), which has been accepted by subsequent authors (Johnston, 1847; Busk, 1854; Hincks, 1880*a*) as being the species they knew as *Cellepora pumicosa*. It is true that Pallas founded his *M. pumicosa* on more than one species, but this does not prevent availability of his name (International Rules, Art. 17 [2]). The *Cellepora pumicosa* of Linnaeus (1767 : 1286) was a branching form, and certainly not that described by Ellis or later authors, and his selection must be disregarded. Johnston (1847), Gray (1848) and Busk (1854) themselves evidently grouped more than

one species under the name *Cellepora pumicosa*, see Lagaaij (1952 : 131), but none of these was branched, and one of them was certainly the species redescribed by Hincks. Busk (1854, Pl. CX, figs. 5–6) gave clear illustrations which define the species he intended (it is impossible to accept Lagaaij's view that these depict *Cellepora armata* Hincks), and the position may be regarded as having finally been stabilized by Hincks (1880). Thus the identity of the species known as *Cellepora pumicosa* is not in doubt. It is so obviously not the one described by Linnaeus, that it now seems surprising that he should have been credited with the species by Hincks. Recent writers have used the attribution " Hincks " or " *auctt. non* Linnaeus ", with the inherent implication that *Cellepora pumicosa* as used was an invalid name. The situation is rectified by restoring Pallas' authorship, excluding *Cellepora pumicosa* Linnaeus (1767) from the recognized synonymy of the species, and regarding Hincks as having selected the species to which the name should apply.

Final stabilization of this species requires the designation of a type specimen. NEOTYPE (here chosen): British Museum (Natural History) 1899.5.1.1301, specimen 3 (on piece of shell); South Devon.

C. pumicosa appears to be referable to *Celleporaria* Lamouroux (1821) as defined by Harmer (1957 : 663). Harmer's revival of *Celleporaria*, to replace *Holoporella* Waters, was a matter of priority, but his change of type-species is unacceptable. He proposed (p. 663, footnote) that, since Bassler (1935 : 68) had stated that *Cellepora cristata* Lamarck, type-species of *Celleporaria*, was unrecognizable, another genosyntype (*C. oculata* Lamarck) should be chosen as type-species. This is not in accordance with the International Rules, and is, moreover, unnecessary, for he proceeded to state (p. 663) that Lamouroux' figure " leaves little doubt " that *C. cristata* is identical with *C. repleta* (Waters). If Harmer recognized *C. cristata* rightly, it is congeneric with *C. oculata*, and his definition of *Celleporaria* can be retained with the correct type-species.

Pouyet's (1963 : 12) reason for preferring *Holoporella* Waters (1909) to *Celleporaria* Lamouroux is inadmissible. If definition, rather than type-species, were to be taken as the criterion of recognition for a genus, then most of those introduced before the mid-nineteenth century would have to be abandoned!

401 *C. ramulosa*, Linnaeus: ***Omalosecosa ramulosa*** (Linnaeus, 1767).

Type-species by original designation of *Omalosecosa* Canu & Bassler (1925).

403 *C. dichotoma*, Hincks: ***Buskea dichotoma*** (Hincks, 1862).

Type-species by original designation of *Harmerella* Lagaaij (1952 : 140), which appears, however, to be a junior subjective synonym of *Buskea* Heller (1867), type-species by monotypy: *Buskea nitida* Heller, 1867.

Var. α (*attenuata*, Alder): var. ***attenuata*** Alder, 1864.

406 *C. avicularis*, Hincks: ***Turbicellepora avicularis*** (Hincks, 1860).

For discussion of this genus and the reasons for its establishment, see Ryland (1963*b* : 33).

Pouyet (1965) proposes to retain *Schismopora* P. H. MacGillivray, for this and related species, by altering the type-species (*Cellepora costata* MacGillivray, selected by Gregory, 1893), as suggested by Harmer (1957 : 908). It should be noted, however, that a valid choice of type-species can be revoked only by decision of the International Commission on Zoological Nomenclature.

409 *C. tubigera*, Busk: ***Turbicellepora tubigera*** (Busk, 1859).

410 *C. armata*, Hincks: ***Turbicellepora armata*** (Hincks, 1860).

411 *C. Costazii*, Audouin: ***Celleporina hassallii*** (Johnston, 1847).

Harmer (1957 : 901) has shown that the British species *C. hassallii*, type-species by monotypy of *Celleporina* Gray (1848), is different from though congeneric with *C. costazii* (Audouin, 1826).

Var. α (*tubulosa*): var. **tubulosa** Hincks, 1880.

414 *Celleporella lepralioides*, Norman: ***Lagenipora lepralioides*** (Norman, 1868).

For discussion, see 235 *Lagenipora socialis*, Hincks.

415 *C. pygmaea*, Norman: ***Lagenipora pygmaea*** (Norman, 1869).

For discussion of this species and its generic placing, see Ryland (1963*b* : 30).

CYCLOSTOMATA

419 *Crisia cornuta*, Linnaeus: ***Crisidia cornuta*** (Linnaeus, 1758).

Type-species by original designation of *Crisidia* Milne Edwards (1838).

Var. α (*geniculata*): ***Filicrisia geniculata*** (Milne Edwards, 1838). Type-species by monotypy of *Filicrisia* d'Orbigny (1853 : 604).

420 *C. eburnea*, Linnaeus: ***Crisia eburnea*** (Linnaeus, 1758).

Type-species of *Crisia* Lamouroux (1812 : 183), see Harmer (1923).

Var. α (*aculeata*, Hassall): ***Crisia aculeata*** Hassall, 1841. Harmer (1891) has amplified the description of this and other British species.

Var. β (*producta*, Smitt): ***Crisiella producta*** (Smitt, 1865). Type-species by original designation of *Crisiella* Borg (1924). There appear to be no definite British records of *C. producta* .

422 *C. denticulata*, Lamarck: ***Crisia denticulata*** (Lamarck, 1816).

Var. α: ***Crisia ramosa*** Harmer, 1891.

425 *Stomatopora granulata*, M.-Edwards: ***Stomatopora trahens*** (Couch, 1841).

The species described by Hincks is not *Alecto granulata* Milne Edwards (1838), see Lagaaij (1963 : 208), but *Tubulipora trahens* Couch. Couch described the species a second time (1844 : 105) and illustrated it in Pl. IX, fig. 5 (not fig. 3 as stated in the text, see Gregory, 1896 : 48, footnote).

427 *S. major*, Johnston: ***Diaperoecia major*** (Johnston, 1847).

Referred to *Diaperoecia* Canu (1918) by O'Donoghue & O'Donoghue (1926 : 23). Description amplified by Hastings (1963 : 122).

429 *S. dilatans*, Johnston: ***Oncousoecia dilatans*** (Johnston, 1847).

Type-species of *Oncousoecia* Canu (1918 : 325), designated by Osburn (1933).

Supplementary description given by Hastings (1963 : 117).

430 *S. Johnstoni*, Heller: ***Diaperoecia johnstoni*** (Heller, 1867).

Referred to *Diaperoecia* by O'Donoghue & O'Donoghue (1926).

Var. α (*robusta*). No information.

432 *S. expansa.*

Preoccupied by *Stomatopora* [referred to *Tubulipora* by Borg, 1933 : 518] *expansa* Packard (1863 : 406), see Jelly (1889 : 255).

433 *S. incurvata*, Hincks: ***Stomatopora incurvata*** (Hincks, 1860).

Introduced as a nomen nudum (Hincks, 1858). The form described by Balavoine (1958 : 56, Pl. I, fig. 6) as *Stomatoporina Roberti Lamii* gen. et sp. n. falls within the range of variation recorded for the present species by Hincks and evident in specimens in the collections of the British Museum (Natural History) (P. L. Cook, pers. comm.). I regard Balavoine's species as being synonymous with *S. incurvata.*

434 *S. diastoporides*, Norman: ***Oncousoecia diastoporides*** (Norman, 1869).

Referred to *Oncousoecia* Canu (1918) by Osburn (1933).

435 *S. compacta*, Norman. No additional information.

436 *S. incrassata*, Smitt: ***Proboscina incrassata*** Smitt, 1865.

Referred back to *Proboscina* Audouin (1826) by O'Donoghue & O'Donoghue (1926).

437 *S. deflexa*, Couch: ***Entalophora deflexa*** (Couch, 1841).

There seems little doubt that, as proposed by Marcus (1950 : 6), *Entalophora clavata* (Busk, 1859) described by Hincks on p. 456 is a junior synonym of the present species.

438 *S. fungia*, Couch: ***Tubulipora penicillata*** (Fabricius, 1780).

The conspecificity of *Tubulipora fungia* Couch (1841 : 72) with *Tubulipora penicillata* Fabricius (1780 : 429), suspected by Nordgaard (1918), is accepted by Kluge (1962 : 104).

441 *S. fasciculata*: ***Filifascigera fasciculata*** (Hincks, 1880).

Referred to *Filifascigera* d'Orbigny (1853 : 684) by Osburn (1953).

444 *Tubulipora lobulata*, Hassall: ***Tubulipora lobifera*** Hastings, 1963.

The species described by Hincks is not *T. lobulata* Hassall (1841), see Hastings (1963*a*); also, fig. 5–5a on Pl. LXI illustrates not this species but *Oncousoecia dilatans.*

446 *T. flabellaris*, Fabricius: ***Tubulipora phalangea*** Couch, 1844.

T. flabellaris (Fabricius, 1780) is probably not a British species (Harmer, 1898); see also p. 244.

448 *T. fimbria*, Lamarck: ***Tubulipora plumosa*** Harmer, 1898.

For discussion of identity of British species, see Harmer (1898); for discussion of authorship of *T. plumosa*, see Ryland (1963*b*).

451 *Idmonea Atlantica*, E. Forbes: ***Idmidronea atlantica*** (Forbes in Johnston, 1847).

Placed by Borg (1944) in *Idmidronea* Canu & Bassler (1920), and not as claimed by Kluge (1962) the type-species of *Idmonea*, which is a synonym of *Tubulipora* Lamarck (1816) (see Harmer, 1898 : 86; Borg, 1944 : 32).

Var. α (*tenuis*, Busk): ***Idmidronea flexuosa*** (Pourtales, 1867). As pointed out by Osburn (1953), the identity of var. *tenuis* Busk (1875) with *Idmonea flexuosa* Pourtales cannot be regarded as absolutely certain. There are no British records.

453 *I. serpens*, Linnaeus: **Tubulipora liliacea** (Pallas, 1766).

Identity recognized by Harmer (1898).

Var. α (*radiata*). No information.

456 *Entalophora clavata*, Busk: **Entalophora deflexa** (Couch, 1841).

See 437 *Stomatopora deflexa*, Couch.

458 *Diastopora patina*, Lamarck: **Berenicea patina** (Lamarck, 1816).

For use and validity of *Berenicea* Lamouroux (1821), see Buge (1957 : 62).

462 *D. obelia*, Johnston: **Diplosolen obelia** (Johnston, 1838).

Type-species by original designation of *Diplosolen* Canu (1918).

463 *D. Sarniensis*, Norman: **Berenicea sarniensis** (Norman, 1864).

464 *D. suborbicularis*: **Berenicea suborbicularis** (Hincks, 1880).

468 *Hornera lichenoides*, Linnaeus: **Hornera lichenoides** (Linnaeus, 1758).

469 *H. violacea*, Sars: **Stegohornera violacea** (M. Sars, 1863).

Type-species by monotypy of *Stegohornera* Borg (1944 : 177).

473 *Lichenopora hispida*, Fleming: **Disporella hispida** (Fleming, 1828).

Type-species by monotypy of *Disporella* Gray (1848), reintroduced by Borg (1944). See also *D. venabulum* (p. 245).

Var. α (*meandrina*, Peach). No information.

Var. β: **Disporella mamillata** (Lagaaij, 1952). Appears to be congeneric with *D. hispida* (Fleming).

476 *L. radiata*, Audouin: **Lichenopora radiata** (Audouin, 1826).

478 *L. verrucaria*, Fabricius: **Lichenopora verrucaria** (Fabricius, 1780).

479 *L. regularis*, D'Orbigny: **Actinopora stellata** (Koch & Dunker, 1837).

The type-species of *Actinopora* d'Orbigny (1853 : 762) is *A. regularis* d'Orbigny (1853) designated by Gregory (1896 : 174), but which was placed by Gregory (1909 : 21) under the synonymy of *Ceriopora stellata* Koch & Dunker (1837).

481 *Domopora stellata*, Goldfuss: **Domopora truncata** (Fleming, 1828).

According to Gregory (1909 : 277–279), the species described by Hincks is different from the one named by Goldfuss (1826: 39). Fleming (1828) introduced *Tubulipora truncata*, noting specifically that it was not *Myriapora truncata* Pallas (1766). From his description it is quite clear that the species intended was that later called *Domopora stellata* by Hincks.

485 *D. truncata*, Jameson.

If, as Hincks maintained, this is a distinct species, it requires a new name. The name *truncata* was not introduced by Jameson (1811), who merely recorded *Millepora truncata* Linnaeus (1767) from the Shetland Islands. Reference to Linnaeus (1767) shows that the species concerned is *Myriapora truncata* Pallas (1766), which definitely does not occur in the Shetland Islands. (The validity of *Myriapora* is upheld by Lagaaij, 1952). Jameson's species was, presumably, the one later and quite properly described as *Tubulipora truncata* by Fleming (see above).

486 *Tubulipora hyalina*, Couch. Unrecognizable.

CTENOSTOMATA

491 *Alcyonidium gelatinosum*, Linnaeus: ***Alcyonidium gelatinosum*** (Linnaeus, 1767).

Type-species by monotypy, through its junior synonym *A. diaphanum* Lamouroux (1813), of *Alcyonidium* Lamouroux (1813). Kluge (1962 : 189) distinguishes a var. *diaphanum*, attributed to Farre (1837), which is incorrect. *A. gelatinosum* as described by Hincks, probably also includes *A. proliferans* Lacourt (1951), which may in fact only be a growth form (see p. 243).

493 *A. hirsutum*, Fleming: ***Alcyonidium hirsutum*** (Fleming, 1828).

495 *A. mamillatum*, Alder: ***Alcyonidium mamillatum*** Alder, 1856.

496 *A. lineare*, Hincks.

Borg's (1933 : 546) view that this is a growth form of *A. mamillatum* is accepted by Prenant & Bobin (1956 : 199).

497 *A. disjunctum*, Hincks: ***Alcyonidium disjunctum*** Hincks, 1877.

No additional information.

498 *A. mytili*, Dalyell: ***Alcyonidium mytili*** Dalyell, 1848.

The status of *A. mytili* possibly deserves further study, but I list it here in the sense defined by Prenant & Bobin (1956 : 217) and Matricon (1960).

500 *A. albidum*, Alder: ***Alcyonidium albidum*** Alder, 1856.

501 *A. polyoum*, Hassall: ***Alcyonidium polyoum*** (Hassall, 1841).

502 *A. parasiticum*, Fleming: ***Alcyonidium parasiticum*** (Fleming, 1828).

504 *A. radiatum*, Alder, MS. A *nomen nudum*.

506 *Flustrella hispida*, Fabricius: ***Flustrellidra hispida*** (Fabricius, 1780).

Type-species by original designation of *Flustrellidra* Bassler (1953) pro *Flustrella* Gray (1848), preoccupied by *Flustrella* Ehrenberg (1839 : 90).

509 *Arachnidium hippothooides*, Hincks: ***Arachnidium hippothooides*** Hincks, 1859.

Type-species by monotypy of *Arachnidium* Hincks (1859).

510 *A. clavatum*, Hincks: ***Arachnidium clavatum*** Hincks, 1877.

511 *A. fibrosum*: ***Arachnidium fibrosum*** Hincks, 1880.

513 *Vesicularia spinosa*, Linnaeus: ***Vesicularia spinosa*** (Linnaeus, 1767).

Type-species of *Vesicularia* J. V. Thompson (1830), discussed by Harmer (1915 : 61).

516 *Amathia lendigera*, Linnaeus: ***Amathia lendigera*** (Linnaeus, 1767).

Type-species by monotypy of *Amathia* Lamouroux (1812 : 184.)

519 *Bowerbankia imbricata*, Adams: ***Bowerbankia imbricata*** (Adams, 1800).

Type-species by monotypy, through its junior synonym *B. densa* Farre (1837), of *Bowerbankia* Farre (1837). *B. densa* is a growth form of *B. imbricata*.

521 *B. caudata*, Hincks: ***Bowerbankia gracilis*** Leidy, 1855.

Synonymy of *Valkeria caudata* Hincks (1877 : 215) with *B. gracilis* Leidy was accepted by Bobin & Prenant (1954).

522 *B. pustulosa*, Ellis & Sol.: ***Bowerbankia pustulosa*** (Ellis & Solander, 1786).

524 *B. citrina*, Hincks: ***Bowerbankia citrina*** (Hincks, 1877).

525 *B. gracillima*, Hincks: ***Bowerbankia gracillima*** (Hincks, 1877).

527 *Avenella fusca*, Dalyell: ***Avenella fusca*** Dalyell, 1848.

Type-species by monotypy of *Avenella* Dalyell, 1848.

529 *Farrella repens*, Farre: ***Farrella repens*** (Farre, 1837).

Type-species of *Farrella* Ehrenberg (1839, Table 2, following p. 120) pro *Lagenella* Farre (1837 : 403), preoccupied, of which it was type by monotypy.

Form *elongata*. A growth form according to Marcus (1926 : 50), a conclusion accepted by Prenant & Bobin (1956) and Miss P. L. Cook (pers. comm.). I do not follow Osburn & Soule (1953), therefore, in regarding *Farrella elongata* (van Beneden, 1845[a]) as a species.

532 *Buskia nitens*, Alder: ***Buskia nitens*** Alder, 1856.

Type-species by monotypy of *Buskia* Alder (1856).

535 *Cylindroecium giganteum*, Busk: ***Nolella stipata*** Gosse, 1855.

Type-species by monotypy of *Nolella* Gosse (1855 : 35). Harmer (1915 : 52) recognized that *Cylindroecium* Hincks (1880*a*) was a synonym of *Nolella* Gosse, though it was uncertain from the original description whether Gosse's name applied to the present species or to the following one: he thought the former. If the generic name *Nolella* is to be employed, so must the name *stipata*, which antedates *gigantea* Busk (1856), as in Osburn & Soule (1953) (cf. Prenant & Bobin, 1956).

536 *C. dilatatum*, Hincks: ***Nolella dilatata*** (Hincks, 1860).

537 *C. pusillum*: ***Nolella pusilla*** (Hincks, 1880).

Redescribed by Ryland (1958*b*).

539 *Anguinella palmata*, Van Beneden: ***Anguinella palmata*** van Beneden, 1845.

Type-species by monotypy of *Anguinella* van Beneden (1845[b]).

540 *Nolella stipata*, Gosse: ***Nolella stipata*** Gosse, 1855.

See 535 *Cylindroecium giganteum* (above).

543 *Triticella flava*, Dalyell: ***Triticella flava*** Dalyell, 1848.

Type-species by monotypy of *Triticella* Dalyell (1848).

545 *T. Korenii*, G. O. Sars: ***Triticella korenii*** G. O. Sars, 1874.

T. Boeckii, Sars (in text) is a synonym (Silén, 1936).

547 *T. pedicellata*, Alder: ***Triticella pedicellata*** (Alder, 1856).

548 *Lagenella nutans* (mentioned in text). See *Mimosella verticillata* (p. 244).

549 *Hippuraria Egertoni*, Busk: ***Triticella korenii*** G. O. Sars, 1874.

Identity recognized by Waters (1910 : 241, footnote) and further discussed by Harmer (1915 : 90).

551 *Valkeria uva*, Linnaeus: ***Walkeria uva*** (Linnaeus, 1758).

Type-species by monotypy, through its junior synonym *W. cuscuta* (Linnaeus), of *Walkeria* Fleming (1823) (f. *cuscuta* is a condition of growth of *W. uva*). The generic name was spelled *Walkeria* when introduced (Fleming, 1823), but altered to *Valkeria* by the same author in a later work (Fleming, 1828). In accordance with Art. 32 (a) and Appendix C 11 of the International Code of Zoological Nomenclature, the original spelling should be used.

554 *V. tremula*, Hincks: ***Walkeria tremula*** Hincks, 1862.

556 *Mimosella gracilis*, Hincks: ***Mimosella gracilis*** Hincks, 1851.

Type-species by monotypy of *Mimosella* Hincks (1851).

561 *Victorella pavida,* Saville Kent: ***Victorella pavida*** Kent, 1870.
Type-species by monotypy of *Victorella* Kent (1870). Compare *Tanganella muelleri* (p. 243), which is very similar—possibly identical.

ENTOPROCTA

565 *Pedicellina cernua,* Pallas: ***Pedicellina cernua*** (Pallas, 1774).
Hincks' citation of Pallas (1771 [actually 1778]) for the original description is incorrect. Type-species of *Pedicellina* by monotypy: *P. echinata* M. Sars (1835), a synonym of *Brachionus cernuus* Pallas.
Var. α (*glabra*). Glabrous form of *P. cernua* (discussed by Prenant & Bobin, 1956 : 102).

567 *P. nutans,* Dalyell: ***Pedicellina nutans*** Dalyell, 1848.
Description amplified by Ryland (1961*a*).

570 *P. gracilis,* Sars: ***Barentsia gracilis*** (M. Sars, 1835).
Referred by Hincks (1887) to *Barentsia* Hincks (1880*c*). Compare *B. benedeni* (p. 245).

573 *Loxosoma singulare,* Keferstein: ***Loxosomella fauveli*** Bobin & Prenant, 1953.
L. singulare is type-species of *Loxosoma* Keferstein (1862) by monotypy; but the species described by Hincks, and again by Atkins (1932), is not Keferstein's species. See also Prenant & Bobin (1956 : 78).

574 *L. phascolosomatum,* Carl Vogt: ***Loxosomella phascolosomata*** (Vogt, 1876).
Referred to *Loxosomella* gen. n. by Mortensen (1911).

575 *L. claviforme*: ***Loxosomella claviformis*** (Hincks, 1880).
Referred to *Loxosomella* Mortensen by Bobin & Prenant (1953).
There have been numerous additions in the genera *Loxosoma* and *Loxosomella,* see p. 245.

PTEROBRANCHIA

580 *Rhabdopleura Normani,* Allman: ***Rhabdopleura normani*** Allman, 1869.
Type-species by monotypy of *Rhabdopleura* Allman (1869).

581 *Rhabdopleura compacta*: ***Rhabdopleura compacta*** Hincks, 1880.
For validity see Stebbing (1968).

3. ADDITIONAL SPECIES RECORDED AROUND THE BRITISH ISLES

In certain cases, Hincks described under one name two forms now recognized as specifically distinct. These have been dealt with in the main section of the Index (as in 14, *Eucratea chelata* and 317, *Umbonella verrucosa*). On the other hand, there are species which have been described subsequently and were not covered by Hincks in a definitely recognizable manner (e.g. *Crisia ramosa*), or not at all (e.g. *Conopeum seurati* and *Hypophorella expansa*); and some have been introduced to Britain subsequently (e.g. *Bugula neritina.*) These are regarded as additional species and are included in the list which follows.

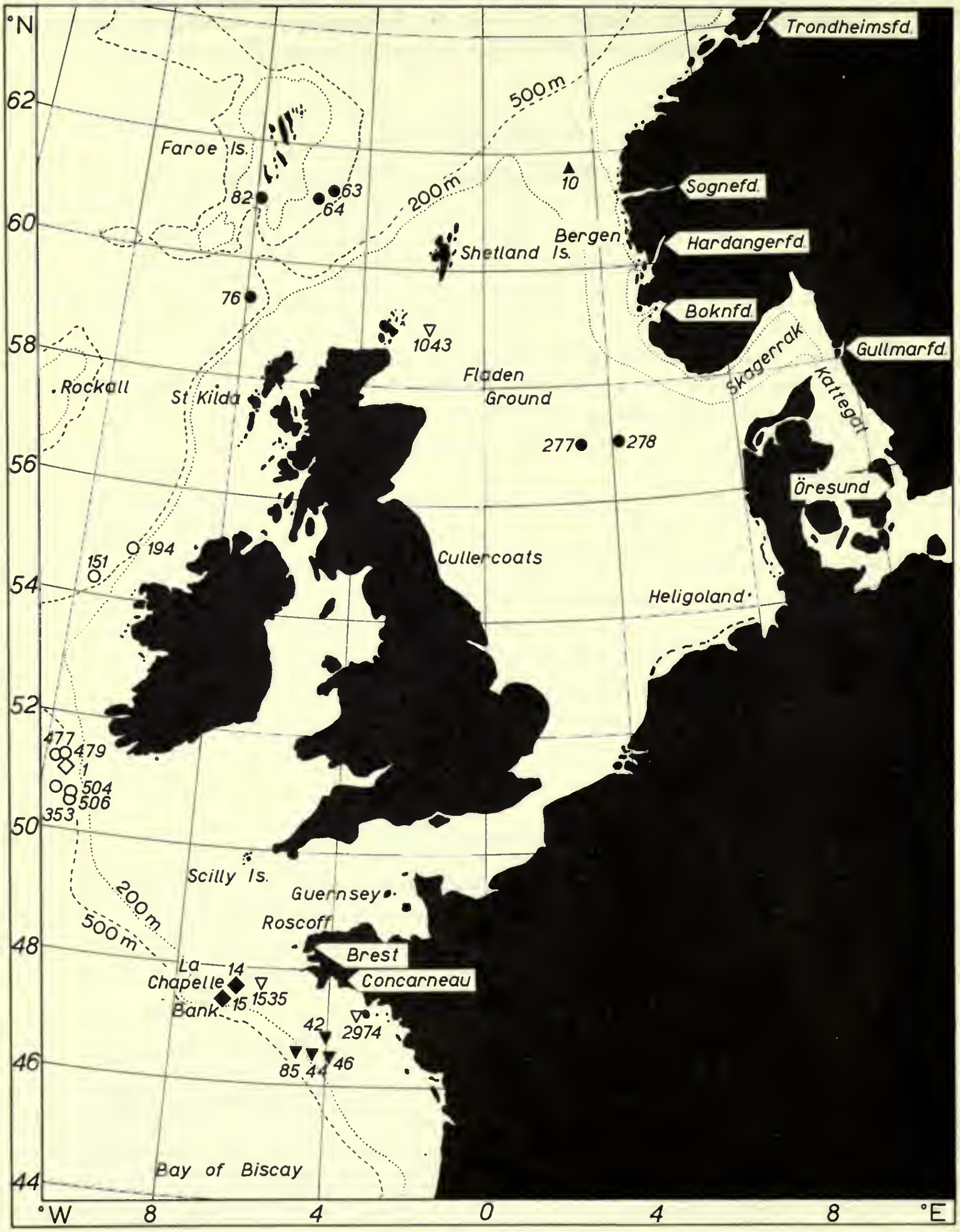
°N
62
60
58
56
54
52
50
48
46
44
°W
8
4
0
4
8
°E
Trondheimsfd.
500 m
Faroe Is.
82
63
64
10
Sognefd.
200 m
Bergen
Hardangerfd.
Shetland Is.
76
Boknfd.
1043
Skagerrak
Gullmarfd.
Fladen
Ground
Rockall
St Kilda
Kattegat
277
278
Öresund
194
151
Cullercoats
Heligoland
477
479
1
504
506
353
Scilly Is.
Guernsey
200 m
500 m
Roscoff
Brest
Concarneau
La
Chapelle
Bank
14
15
1535
42
2974
85
44
46
Bay of Biscay

FIG. 4.

It would be neither practicable nor sensible, when dealing with a group of marine animals, to restrict the definition of " British " to coastal or territorial waters, particularly as a number of interesting records come from the deep water of the continental slope. Accordingly, the southern and northern limits of the area covered have been drawn at 46° and 62° N respectively.

The southern boundary at 46° N allows inclusion of the entire Brittany peninsula, with its marine stations at Dinard, Roscoff and Concarneau. This is a logical step from the traditional acceptance of the Channel Islands as part of the British area. In addition, it includes that section of the continental slope from which, in recent

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FIG. 4. Position of stations yielding polyzoa new to the British fauna, and of other localities referred to in the text.

▲ Norwegian North Atlantic Expedition (Nordgaard, 1900).
10 : 61° 41′ N, 3° 19′ E; 402 m.

● " Michael Sars " (Nordgaard, 1907).
63 : 61° 21′ N, 5° 12′ W; 357 m.
64 : 61° 10′ N, 5° 46′ W; 290 m.
76 : 59° 23′ N, 7° 50′ W; 1100 m.
82 : 61° 9′ N, 7° 54′ W; 330 m.
277 : 57° 6′ N, 2° 58′ E; 68 m.
278 : 57° 4′ N, 4° 14′ E; 65 m.

○ Irish investigations (Nichols, 1911).
151 : 54° 17′ N, 11° 33′ W; 719 m.
194 : 54° 49′ N, 10° 30′ W; 679 m.
353 : 50° 37′–50° 40′ N, 11° 32′ W; 457–991 m.
477 : 51° 15′ N, 11° 47′ W; 1293–1300 m.
479 : 51° 20′ N, 11° 41′ W; 656–1024 m.
504 : 50° 42′ N, 11° 18′ W; 1146–1432 m.
506 : 50° 34′ N, 11° 19′ W; 1207–1227 m.

◇ Deep-sea trawling (Kirkpatrick, 1889).
1 : approx. 50° 50′ N, 11° 26′ W; 576 m.

▼ " L'Hirondelle " (Jullien & Calvet, 1903).
(Longitudes refer to Greenwich, see p. 238.)
42 : 46° 47′ N, 3° 52′ 30″ W; 136 m.
44 : 46° 27′ N, 4° 10′ W; 166 m.
46 : 46° 25′ N, 3° 35′ 30″ W; 155 m.
85 : 46° 31′ N, 4° 32′ W; 180 m.

▽ " Princess Alice II ", " L'Hirondelle II " (Calvet, 1931).
1043 : 59° 03′ N, 1° 48′ W; 88 m.
1535 : 47° 46′ N, 5° 40′ W; 132 m.
2974 : off Belle-Ile; 85 m.

◆ " Vienne " on La Chapelle Bank (Guérin-Ganivet, 1911*a*).
14 : 47° 37′ N, 6° 30′ W; 200 m.
15 : 47° 30′ N, 6° 50′ W; 400 m.

years, collections of Polyzoa have been made by R. V. "Sarsia" (Ryland, in preparation).

The northern boundary at 62° N passes clear of the Shetland Islands to the Norwegian coast at Nordfjorden. The well-studied area around Bergen is on the same latitude as Shetland. The Faroe Islands, which straddle latitude 62° N, have also been included.

The natural western boundary follows the continental slope (the 1500 m. isobath approximately sets the limit at the present time) from Faroe, west of Faroe Bank, Rockall Bank and Porcupine Bank, then across the Western Approaches into the Bay of Biscay. The eastern boundary lies at 14° E, which includes the Öresund and Kiel Bay within the area, but excludes the Baltic Sea.

A small number of High Arctic species, that do not occur in Norway south of the Lofoten Islands, have been recorded from the Faroe Islands (Kramp, 1934)—apparently colonized from Greenland and Iceland via the North Atlantic Transversal Ridge. Further southward spread by way of the Wyville Thomson Ridge to northern Scotland might also be possible, and one species (*Celleporina surcularis*) may perhaps have reached the Shetland Islands by this route (see comment on p. 242).

Many of the records, particularly from deep water, come from the reports of research ships, and the positions of relevant stations are indicated in Text-fig. 4, together with other localities mentioned in this list. (It should be noted that Jullien & Calvet, 1903, like Calvet, 1907, and Guérin–Ganivet, 1911*a*, measure longitude with reference to the Paris meridian, 2° 20′ 14″ east of Greenwich).[1]

Some of the species listed are very imperfectly known, and the generic placing may be rather conjectural. In square brackets one or more references to descriptions follows the name, and then come details of the occurrence of the species.

POLYZOA

CHEILOSTOMATA (ANASCA)

Membranipora tenuis Desor, 1848 [Marcus, 1940 : 126; Prenant & Bobin, 1966 : 120].

Present in the Öresund (Levinsen, 1894; Marcus, 1940).

Membranipora tuberculata (Bosc, 1802) [Prenant & Bobin, 1966 : 115].

Washed up on Sargassum weed at Brest (Guérin-Ganivet, 1911*b*, as *M. tehuelcha*).

Conopeum seurati (Canu, 1928) [Prenant & Bobin, 1966 : 1207].

In brackish water, east, south and west coasts of Britain (Markowski, 1960, as *C. spiculatum*; Cook, 1962).

Sarsiflustra abyssicola (M. Sars in G. O. Sars, 1872) [Kluge, 1962 : 319; Prenant & Bobin, 1966 : 173].

Taken by the "Michael Sars" off the north-west of Scotland, St. 76 (Nordgaard, 1907). Type-species by monotypy of *Sarsiflustra* Jullien (Jullien & Calvet, 1903 : 43).

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[1] My attention was drawn to this by Miss P. L. Cook.

Chartella calveti (Guérin-Ganivet, 1911) [Prenant & Bobin, 1966 : 193].

Occurs in shallow water in the Brest–Roscoff area. Placed by Prenant & Bobin in *Terminoflustra*, but see the comment on this genus under 122 (p. 212).

(?) *Crassimarginatella tensa* (Norman, 1903 : 595).

Dredged from fjords around Bergen and in Hardangerfjorden, and described as *Oochilina tensa*. The correct generic placing is not clear, but *Oochilina* is a junior objective synonym of *Crassimarginatella* Canu (1900).

Alderina aquitanica (Jullien, 1903) [Jullien & Calvet, 1903 : 45; Prenant & Bobin, 1966 : 214].

Off Brittany, St. 42. Described as *Biflustra aquitanica*, but Prenant & Bobin appear correct in referring the species to *Alderina* Norman.

Callopora rylandi Bobin & Prenant, 1965 [Prenant & Bobin, 1966 : 231].

Description based on specimens from Roscoff. Material from the Channel Islands is present in the British Museum (Natural History). Recently discovered in south-west Wales.

Tegella arctica (d'Orbigny, 1853) [Kluge, 1962 : 280].

Faroe Islands (Kramp, 1934).

Tegella armifera (Hincks, 1880) [Kluge, 1962 : 276; Prenant & Bobin, 1966 : 242].

Dredged to the east of the Orkney Islands, St. 1043 (Calvet, 1931).

Cauloramphus cymbaeformis (Hincks, 1877) [Kluge, 1962 : 298].

Faroe Islands (Kramp, 1934).

Chlidonia pyriformis (Bertoloni, 1810) [Levinsen, 1909 : 197, as *C. cordieri*].

Calvados (Normandy) (Busk, 1884 : 8, as *C. cordieri*).

Doryporella reticulata Ryland, 1963 [Ryland, 1963*b* : 9].

Bergen, where Korsfjorden meets the Atlantic, 75–180 m.

Calpensia nobilis (Esper, 1796) [Prenant & Bobin, 1966 : 337].

Guernsey (Norman, 1907, as *Micropora impressa*); La Chapelle Bank (Guérin-Ganivet, 1911*a*, as *M. impressa*). For taxonomic discussion see under 174 (p. 216).

Scrupocellaria elongata (Smitt, 1868) [Kluge, 1962 : 382, as *S. arctica*; Prenant & Bobin, 1966 : 409].

The var. *congesta* Norman (1903) was found in shallow water near Bergen (Ryland 1963*b* : 12, with a note on the name of the species).

Scrupocellaria grimaldii Jullien, 1903 [Jullien & Calvet, 1903 : 34; Prenant & Bobin, 1966 : 405].

Off Brittany, St. 42 and 85. It seems almost certain that this is actually *S. inermis* Norman (Hincks, 1880 : 46), but slight doubt remains as Jullien's illustration appears to indicate the presence of a single axillary vibraculum.

Scrupocellaria intermedia Norman, 1893 [Kluge, 1962 : 378; Prenant & Bobin, 1966 : 431].

The southernmost Norwegian record is from Trondheimsfjorden (Norman, 1893), but the species was identified by Nichols (1911 : 9) from St. 151, 353 and 477.

Notoplites harmeri Ryland, 1963 [Ryland, 1963*b* : 15].

Bergen, where Korsfjorden meets the Atlantic, 75–180 m.

Notoplites smitti (Norman, 1868) [Kluge, 1962 : 371].

A High Arctic species recorded, presumably in error, by Nichols (1911). However, Prenant & Bobin (1966 : 446) can hardly be correct in stating that *Notoplites jeffreysii* is the species intended, since Nichols observed a fork-shaped scutum.

Nordgaardia pusilla (Nordgaard, 1907).

" Michael Sars " St. 76 (Nordgaard, 1907 : 5). Described as *Synnotum pusillum*, but Kluge (1962 : 362) created for it the new genus *Nordgaardia*.

Dendrobeania elongata (Nordgaard, 1906) [Kluge, 1962 : 345, as *Bugula*; Prenant & Bobin, 1966 : 479]. (See addendum.)

The original specimen came from Boknfjorden, Stavanger, 140–343 m., which is still the most southerly known locality.

Dendrobeania fruticosa (Packard, 1863) [Kluge, 1962 : 331; Prenant & Bobin, 1966 : 476].

No British records were included by Hincks (1880 : 92), but the species has been recorded off Cullercoats, Northumberland, by Roper (1913 : 38), and further east in the northern North Sea (" Michael Sars " St. 278, Nordgaard, 1907). Also Faroe Islands (Kramp, 1934). Var. *quadridentata* Lovén in Smitt, 1868 [Kluge, 1962 : 333] was recorded earlier by Nordgaard (1900) off the west coast of Norway, St. 10 of the North-Atlantic Expedition, but the synonymy of this var. has become so confused with that of *D. elongata* (Nordgaard, 1906, q.v.), that it is impossible to be sure to which taxon this refers.

Bugula fulva Ryland, 1960 [Ryland, 1960 : 78].

Widely distributed around the British Isles. The range of variation of *B. fulva* is now known (Ryland, 1962) to include the form originally described as *B. aquilirostris*.

Bugula neritina (Linnaeus, 1758) [Ryland, 1960 : 74].

Widely distributed in ports along the south coast of Britain; presumably introduced by shipping.

Bugula simplex Hincks, 1886 [Ryland, 1960 : 91].

Various localities in southern Britain (Ryland, 1958*a*).

Bugula stolonifera Ryland, 1960 [Ryland, 1960 : 78].

Ports in south-west Britain.

Kinetoskias smitti (Danielssen, 1868) [Marcus, 1940 : 194; Prenant & Bobin, 1966 : 545].

Recorded from the fjords of southern Norway (Nordgaard, 1906), the Skagerrak (Silén, 1936) and off the south-west of Ireland (Nichols, 1911, St. 506).

Kinetoskias arborescens (Danielssen, 1868) [Prenant & Bobin, 1966 : 548; Smitt, 1868*a* : 292, 353, Pl. XIX, 28–31, as *Bugula umbella*].

Taken by the Norwegian North-Atlantic Expedition, St. 2, from 1229 m. in Sognefjorden (Nordgaard, 1900). This is the most southerly record.

Erymophora gracilis (Nichols, 1911) [Prenant & Bobin, 1966 : 563].

Recorded by Nichols (1911 : 7; St. 477) off the south-west of Ireland, as *Brettia pellucida* var. *gracilis* nov., later raised to specific level as the type of *Erymophora* gen. n. by Hastings (1943). (See addendum.)

Gephyrotes nitidopunctata (Smitt, 1868) [Kluge, 1962 : 388; Prenant & Bobin, 1966 : 585].

Recorded from various fjords in the Bergen area (Nordgaard, 1906; Ryland, 1963*b*).

CHEILOSTOMATA (*ASCOPHORA*)

Haplopoma planum Ryland, 1963 [Ryland, 1963*a* : 14].

This is the northernmost species of *Haplopoma*, until recently confused with *H. impressum* auctt., which has its southern limit in the Bergen area, Hardangerfjorden, and the Shetland Islands. The " Michael Sars " record, St. 82 (Nordgaard, 1907), presumably belongs to this species.

Hippothoa expansa Dawson [see 291, p. 224] var. *transparens* Roper, 1913.

Northumberland. Almost certainly a growth form of *Celleporella hyalina* (Linnaeus) [271, p. 223], and not of *H. expansa*.

Myriozoella plana (Dawson, 1859) [Kluge, 1962 : 478, as *Schizoporella crustacea* (Smitt)]. (See addendum.)

Myriozoum crustaceum Smitt is type-species by monotypy of *Myriozoella* Levinsen (1909). Faroe Islands (Kramp, 1934, as *Myriozoum crustaceum*).

Schizomavella glebula (Jullien, 1903) [Jullien & Calvet, 1903 : 81].

St. 46. The suboral avicularium and type of ancestrula are characteristic of *Schizomavella* and not *Schizoporella*.

Schizoporella longirostris Hincks, 1886.

Collected recently at several localities among the Isles of Scilly, from 12–51 m. (P. J. Hayward, personal communication and in preparation).

Schizoporella magnifica Hincks, 1886 [Ryland, 1968*b*].

Recorded from two localities in southern Britain.

(?) *Schizoporella nomismata* Jullien, 1903 [Jullien & Calvet, 1903 : 80].

Off Brittany, St. 42. Correct generic placing not clear.

Smittina cervicornis (Pallas, 1766) [Gautier, 1962 : 204].

St. 15, La Chapelle Bank (Guérin-Ganivet, 1911*a*). I agree with Cook (1968) that *Smittina*, rather than *Porella*, is the correct genus for this species.

(?) *Smittina decipiens* Jullien, 1903 [Jullien & Calvet, 1903 : 101, 149].

Taken several times in the Bay of Biscay (Jullien & Calvet, 1903; Calvet, 1931), twice close to the coast of Brittany (Calvet, 1931 : St. 1535 and St. 2974 off Belle-Ile) and also from near the Orkney Islands (St. 1043). Correct generic placing not clear.

Smittoidea grimaldii (Jullien, 1903) [Jullien & Calvet, 1903 : 99, as *Smittia*].

Off Brittany, St. 85. Referable to *Smittoidea* Osburn (1952).

Porella patula (M. Sars, 1851) [Marcus, 1940 : 269].

Occurs in the Bergen area (Ryland, 1963*b*) and extends into the Skagerrak and Kattegat (Silén, 1951). Nordgaard (1912) showed that *Lepralia aperta* Boeck was synonymous with Sars' species. Kluge (1962 : 452), however, employs Boeck's name.

Porella proboscidea Hincks, 1888.

Obtained in the North Sea by the " Michael Sars ", St. 277 (Nordgaard, 1907). There is some doubt as to which species this record actually refers. Kluge (1962) considered that Nordgaard's records of *P. proboscidea* belonged to *P. smitti* Kluge

(1907), though Nordgaard (1918) maintained that he had identified the species correctly.

Phoceana columnaris Jullien, 1903 [Jullien & Calvet, 1903 : 107, 154; Gautier, 1962 : 212].

Recorded by Jullien & Calvet from St. 44.

Escharella ventricosa Hassall, 1842, var. *peristomata* Kluge, 1962 [Ryland, 1963*b* : 26].

Shallow fjords, near Bergen. The status of this taxon requires investigation.

Hemicyclopora multispinata (Busk, 1861).

Recorded by Nichols (1911 : 21) from St. 151, 194 and 504. There is some doubt, however, as to whether this species (and not *H. polita* only) was obtained (Ryland, 1963*b* : 27, footnote). *Mucronella canalifera* Busk (1884) is placed by Cook (1968) under the synonymy of *H. multispinata*.

Marguetta pulchra Jullien, 1903 [Jullien & Calvet, 1903 : 73].

St. 14, La Chapelle Bank (Guérin-Ganivet, 1911*a*).

Bryocryptella torquata (Jullien, 1903) [Jullien & Calvet, 1903 : 77, as *Cryptella*].

St. 14, La Chapelle Bank (Guérin-Ganivet, 1911*a*).

Rhamphostomella ovata (Smitt, 1868) [Kluge, 1962 : 540].

Faroe Islands (Kramp, 1934).

Rhamphostomella plicata (Smitt, 1868) [Kluge, 1962 : 544].

Faroe Islands (Kramp, 1934).

Phidolopora elongata (Smitt, 1868) [Kluge, 1962 : 527, as *Retepora*].

Radösund near Bergen (Nordgaard, 1906). Referred to *Phidolopora* Gabb & Horn by Hansen (1962).

Sertella aquitanica Jullien, 1903 [Jullien & Calvet, 1903 : 60].

St. 15, La Chapelle Bank (Guérin-Ganivet, 1911*a*). The same author records it from the Concarneau region, " où cette espèce n'est pas absolument rare ".

Sertella grimaldii (Jullien, 1903) [Jullien & Calvet, 1903 : 62].

St. 44. Although Jullien (p. 56) did not place this species in *Sertella* gen. n., he stated that it was congeneric with *Retepora cellulosa* Smitt, which Harmer (1933) referred to *Sertella* (see next entry).

Sertella septentrionalis Harmer, 1933 [Kluge, 1962 : 526, as *Retepora cellulosa*; Gautier, 1962 : 233].

St. Kilda (Ryland, 1965*a*). Name proposed by Harmer (1933 : 620) for *Retepora cellulosa* Smitt (1968*b*) non Linnaeus (1758).

Adeonellopsis distoma (Busk, 1859).

St. 14, La Chapelle Bank (Guérin-Ganivet, 1911*a*).

Celleporina surcularis (Packard, 1863) [Kluge, 1962 : 553].

Norman (1907) may have been correct in supposing that his specimen came from the Shetland Islands, as *C. surcularis* has been recorded from the Faroe Islands (Kramp, 1934), though in Norway it is not known to occur south of Tromsö (Nordgaard, 1918).

Turbicellepora coronopus (Wood, 1844) [Gautier, 1962: 260, as *Schismopora*].

Recorded by Jullien & Calvet (1903) from St. 46 and 85. It should be noted that *T. coronopus* was not then being distinguished from *T. tubigera* Busk, and it is uncertain which species was intended (Lagaaij, 1952; Gautier, 1962). Dinard (Balavoine, 1958, 1959).

Turbicellepora coronopusoida (Calvet, 1931) [Calvet, 1931 : 119; Gautier, 1962 : 261, as *Schismopora*].

Included in species list of St. 1043 from near the Orkney Islands, though this station is not mentioned on p. 119. Possibly a mistake, since the species is otherwise only known from the Mediterranean (Gautier, 1962).

Turbicellepora smitti (Kluge, 1962) [Ryland, 1963*b* : 34].

Recorded from the Bergen area (Ryland) and the Kattegat (Smitt, 1868*b*), and from the Faroe-Shetland Channel, "Michael Sars" St. 63 and 64 (Nordgaard, 1907).

Gemellipora eburnea Smitt, 1873 [Busk, 1884 : 5, Pl. XXXIV, 1, as *Pasythea;* Osburn 1940 : 463, Pl. 9, fig. 73–4].

Recorded by Nichols (1911 : 23) St. 151 and 479.

CTENOSTOMATA

Alcyonidium candidum Ryland, 1963 [Ryland, 1963*b* : 36].

Found on stones and on dead *Lophelia* coral from depths exceeding 50 m. in fjords in the vicinity of Bergen.

Alcyonidium proliferans Lacourt, 1951 [Prenant & Bobin, 1956 : 208].

Described from the Dutch coast, but possibly only a form of *A. gelatinosum* (L.) (Hincks, 1880*a* : 491).

Alcyonidium variegatum Prouho, 1892 [Prenant & Bobin, 1956 : 211].

For long only known from a single locality in the Mediterranean (Banyuls), but recently recorded from the Isle of Man (Eggleston, 1963).

Arachnidium simplex Hincks, 1880 [Hincks, 1880*c* : 284; Prenant & Bobin, 1956: 26].

"71 miles W by S from Fastnet, 315 fath." (Kirkpatrick, 1889 : 446).

Immergentia suecica Silén, 1947 [Prenant & Bobin, 1956 : 230].

In dead *Pecten* shells, Gullmarfjorden, Sweden.

(?) *Immergentia* sp. Borings in a shell bearing *Hippothoa divaricata* from Guernsey, 18–27 m. (Brit. Mus. 1897.5.1.792) appear to belong to a species of *Immergentia* (Hastings, personal communication).

Tanganella muelleri (Kraepelin, 1887) [Braem, 1951 : 22].

Braem considered this controversial species sufficiently distinct from *Victorella pavida* Kent to create for it the new genus *Tanganella*. It was found in brackish waters near the Baltic coast of Germany.

Bulbella abscondita Braem, 1951 [Braem, 1951 : 34].

Found by Braem (p. 44) amongst *Victorella pavida* Kent, from London.

Hypophorella expansa Ehlers, 1876 [Prenant & Bobin, 1956 : 272].

Found in the tube lining of the polychaete *Chaetopterus*. First recorded in Britain by Harmer (1897), but now known from a number of localities in the British Isles, and as far north as Trondheim in Norway (Dons, 1939).

Amathia pruvoti Calvet, 1911 [Prenant & Bobin, 1956 : 287].

Found in Chichester Harbour (Stubbings & Houghton, 1964).

Amathia vidovici (Heller, 1867) [Prenant & Bobin, 1956 : 283].

Roscoff (Echalier & Prenant, 1951).

(?) *Bowerbankia pusilla* Jullien, 1903 [Prenant & Bobin, 1956 : 308].

St. 85 (Jullien & Calvet, 1903 : 31).

Penetrantia ditrupae (Norman, 1907) [Prenant & Bobin, 1956 : 324].

Found in the calcified tubes of the serpulid polychaete *Ditrupa arietina* dredged in the Shetland Islands. On the advice of Dr. Anna Hastings I have followed Silén's suggestion (1947 : 38) that Norman's *Terebripora ditrupae* may be a species of *Penetrantia*, though Marcus (1938 : 291) and Prenant & Bobin (1956 : 324) refer it to *Spathipora*. Obviously no placing can be final when based on borings only.

Penetrantia concharum Silén, 1946 [Prenant & Bobin, 1956 : 330].

Living in the dead shells of many species of mollusc, from Gullmarfjorden, Sweden. Recorded from the Isle of Man (Bruce, Colman & Jones, 1963).

Mimosella verticillata (Heller, 1867) [Prenant & Bobin, 1956, 264].

Roscoff (Echalier & Prenant, 1951). Mentioned by Hincks, p. 548, as *Lagenella nutans* Joliet.

Monobryozoon ambulans Remane, 1936 [Prenant & Bobin, 1956 : 335].

Discovered in " Amphioxus sand " off Heligoland.

Monobryozoon limicola Franzén, 1960.

Described from a muddy substratum in Gullmarfjorden, Sweden.

CYCLOSTOMATA

Tubulipora aperta Harmer, 1898 [Harmer, 1898 : 101; Marcus, 1940 : 66; Kluge, 1962 : 96].

Bergen area and the Skagerrak.

Tubulipora flabellaris (Fabricius, 1780) [Harmer, 1898 : 99; Marcus, 1940 : 60; Kluge, 1962 : 91].

The west of Scotland record (O'Donoghue, 1935) may or may not be an error, but there are records from the Skagerrak, Kattegat, Öresund, and from the Heligoland area.

Tervia irregularis (Meneghini, 1847) [Busk, 1875 : 13, Pl. 12, as *Idmonea*].

Appears to be common in the Bay of Biscay below 45° N, and was also recorded by Jullien & Calvet (1903) from St. 44, and by Nichols (1911 : 4) from St. 504.

Bicrisia abyssicola Kluge, 1962 [Ryland, 1967*b* : 270].

St. Kilda (Ryland, 1965*a*); fjords in the Bergen area (Ryland, 1967*b*).

Crisia constans Kluge, 1946 [Kluge, 1962 : 155; Ryland, 1967*b* : 273].

Recorded by Ryland from near Bergen, where Korsfjorden meets the Atlantic, 100–180 m.

Crisia klugei Ryland, 1967 [Kluge, 1962 : 157, as *C. denticulata* var. *borgi*; Ryland, 1967*b* : 275].

The *C. denticulata* of writers on sub-arctic Polyzoa. St. 10 of the Norwegian North-Atlantic Expedition (Nordgaard, 1900); Bergen, where Korsfjorden meets the Atlantic (Ryland, 1967*b*); the Skagerrak (Smitt, 1865).

Crisia ramosa Harmer, 1891 [Harmer, 1891 : 134, 163].

This widely distributed British species was probably the *C. denticulata* var. α of Hincks (1880*a* : 422), but the diagnostic characters, especially of the gonozooid, were not described.

Disporella venabulum Jullien, 1888 [Busk, 1859 : 116, as *Discoporella grignonensis*; Lagaaij, 1952 : 182, as *Lichenopora*].

Recorded (without further discussion) from the region of Dinard by Balavoine (1959 : 13), although his was the first published non-fossil record for this species. The identification was evidently made using Lagaaij (1952), who suspected (p. 182) that the Recent material of *D. hispida* in the British Museum (Natural History) might include specimens of the present species.

(?) *Lichenopora prolifica* Jullien, 1903 [Jullien & Calvet, 1903 : 119].

St. 85. " Both from the description and the figure it seems clear to me that this is no Calyptrostegous species at all, but I am not prepared to say where it ought to be placed " (Borg, 1944 : 234).

ENTOPROCTA

Pedicellina hispida Ryland, 1965 [Ryland, 1965*b* : 200].

Plymouth and Finistère.

Barentsia benedeni (Foettinger, 1886) [Prenant & Bobin, 1956 : 112].

Known from Hull (Ritchie, 1911) and Ostend. Possibly only a form of *B. gracilis* (M. Sars).

Barentsia laxa Kirkpatrick, 1890 [Nielsen, 1964*a* : 57].

Kattegat and Öresund (Nielsen, 1964*a*), Bergen fjords (Nielsen, 1964*b*); Cullercoats (Eggleston & Bull, 1966).

Barentsia mutabilis (Toriumi, 1951) [Ryland, 1961*a*, as *Pseudopedicellina*].

Two localities in Pembrokeshire. *Pseudopedicellina* Toriumi was considered a synonym of *Barentsia* by Ryland (1965*b*).

Loxosoma agile Nielsen, 1964 [Nielsen, 1964*a* : 13].

On *Nicomache trispinata*, Kattegat and Öresund (Nielsen, 1964*a*), and Bergen fjords (Nielsen, 1964*b*).

Loxosoma annelidicola (van Beneden & Hesse, 1864) [Prenant & Bobin, 1956 : 34].

On maldanid polychaetes from the French side of the English Channel; also from Holyhead (Ryland & Austin, 1960).

Loxosoma claparedei Bobin & Prenant, 1953 [Prenant & Bobin, 1956 : 32].

On *Notomastus latericeus*, from Roscoff.

Loxosoma loricatum Harmer, 1915 [Prenant & Bobin, 1956 : 39].

On *Hermione hystrix*, Roscoff.

Loxosoma loxalina Assheton, 1912 [Prenant & Bobin, 1956 : 36].

In the tube of an unidentified maldanid polychaete, Sound of Mull, Scotland.

Loxosoma monensis Eggleston, 1965.

On unidentified worm tube, Isle of Man.

Loxosoma pectinaricola Franzén, 1962.

On *Pectinaria belgica*, Skagerrak to Öresund (Franzén, 1962; Nielsen, 1964*a*) and Bergen fjords (Nielsen, 1964*b*); Cullercoats (Eggleston & Bull, 1966).

Loxosoma rhodinicola Franzén, 1962.

On *Rhodine loveni*, Gullmarfjorden, Sweden. Recorded as *Loxosoma* sp. by McIntyre (1961) on the same host in Loch Nevis and on the Fladen Ground (North Sea, off Aberdeen); also by Nielsen from the Skagerrak and Öresund (1964*a*) and Bergen fjords (1964*b*).

Loxosoma saltans Assheton, 1912 [Prenant & Bobin, 1956 : 36].

In tube of the maldanid polychaete *Leiochone clypeata* (= *Clymene ebiensis*), Sound of Sleat, Skye.

Loxosoma significans Nielsen, 1964 [Nielsen, 1964*a* : 11].

On the maldanid *Asychis significans*, Skagerrak to Öresund (Nielsen, 1964*a*), and Bergen fjords (Nielsen, 1964*b*).

Loxosoma singulare Keferstein, 1862 (non Hincks, 1880*a*) [Prenant & Bobin, 1956 : 29].

On *Notomastus latericeus*, on the French side of the English Channel.

Loxomespilon perezi Bobin & Prenant, 1953 [Prenant & Bobin, 1956 : 40].

On *Sthenelais boa*, Roscoff; Plymouth (Marine Biological Association, 1957).

Loxosomella alata (Barrois, 1877) [Prenant & Bobin, 1956 : 57, as *Loxocalyx*].

On sponge *Dysidea*, Barfleur. I follow Nielsen (1964*a*) in uniting *Loxocalyx* with *Loxosomella*.

Loxosomella antedonis Mortensen, 1911.

Swansea docks (Ryland & Austin, 1960).

Loxosomella aripes Nielsen, 1964 [Nielsen, 1964*b* : 4].

On *Laonice cirrata*, Bergen.

Loxosomella arvyae Bobin & Prenant, 1953 [Prenant & Bobin, 1956 : 81].

On *Phascolion strombi*, Roscoff; Isle of Man (Eggleston, 1965).

Loxosomella atkinsae Bobin & Prenant, 1953 [Prenant & Bobin, 1956 : 92].

On *Phascolion strombi*, Concarneau, Roscoff; Isle of Man (Eggleston, 1965); Kattegat (Nielsen, 1964*a*). Nielsen found that *L. bouxini* was based on the contracted state of *L. atkinsae*.

Loxosomella bouxini Bobin & Prenant, 1953.

See *L. atkinsae*.

Loxosomella brucei Eggleston, 1965.

Attached to the lining of an unidentified worm-tube, Isle of Man.

Loxosomella compressa Nielsen & Ryland, 1961.

On the setae of *Lagisca extenuata*, Bergen; on *L. extenuata* and *Gattyana cirrosa*, Kattegat (Nielsen, 1964*a*); on the former, Isle of Man (Eggleston, 1965) and on both, Cullercoats (Eggleston & Bull, 1966).

Loxosomella crassicauda (Salensky, 1877) [Prenant & Bobin, 1956 : 70].

Type-species by original designation of *Loxosomella* Mortensen, 1911. Plymouth (Atkins, 1932).

Loxosomella cuenoti Bobin & Prenant, 1953 [Prenant & Bobin, 1956 : 94].

On *Phascolion strombi*, Concarneau.

Loxosomella discopoda Nielsen & Ryland, 1961.

On the ophiuroid *Amphilepis norvegica*, Bergen area; Skagerrak (Nielsen, 1964*a*).

Loxosomella elgans Nielsen, 1964 [Nielsen, 1964*a* : 18].

In tubes of *Praxillella praetermissa* and *Rhodine gracilior* from the Kattegat; common in the Bergen area, in tubes of *Praxillella* and *Heterodymene robusta* (Nielsen, 1964*b*).

Loxosomella fagei Bobin & Prenant, 1953 [Prenant & Bobin, 1956 : 95].

On *Hermione hystrix*, Roscoff.

Loxosomella fungiformis Bobin & Prenant, 1953 [Prenant & Bobin, 1956 : 87].

On *Phascolion strombi*, Concarneau; Isle of Man (Eggleston, 1965). Doubtfully distinct from *L. atkinsae* Bobin & Prenant, of which it probably represents a highly contracted state.

Loxosomella glandulifera Franzén, 1962.

In tubes of the polychaete *Panthalis oerstedi* from the Kattegat (Franzén, 1962; Nielsen, 1964*a*).

Loxosomella harmeri (Schultz, 1895) [Nielsen, 1964*a* : 28].

On *Gattyana cirrosa*, from the Kattegat and Öresund; on *Gattyana* and from *Chaetopterus* tubes, Cullercoats (Eggleston & Bull, 1966).

Loxosomella kefersteinii (Claparède, 1867) [Prenant & Bobin, 1956 : 68].

Swansea docks (Ryland & Austin, 1960).

Loxosomella marsypos Nielsen & Ryland, 1961.

In the tube lining of *Eunice pennata*, Bergen; Kattegat (Nielsen, 1964*a*); in tubes of *Chaetopterus variopedatus*, Isle of Man (Eggleston, 1965).

Loxosomella murmanica (Nilus, 1909) [Prenant & Bobin, 1956 : 72].

Nielsen (1967) considers that *L. nitschei* Prenant & Bobin (non Vigelius, see next entry) and *L. murmanica*, which both occur on *Phascolion strombi*, are identical. Widely distributed from the English Channel northwards.

Loxosomella nitschei (Vigelius, 1882) [Ryland, 1961*b* : 35].

Cullercoats (Roper, 1913; Eggleston & Bull, 1966); also Bergen (Ryland, 1961*b*). On various Polyzoa. This is not *L. nitschei* Arvy & Prenant (1952), Prenant & Bobin (1956) or Nielsen (1964*a*)—see *L. murmanica* (above).

Loxosomella nordgaardi Ryland, 1961 [Ryland, 1961*b* : 31].

Described from fjords in the neighbourhood of Bergen; Kattegat (Nielsen, 1964*a*); Cullercoats (Eggleston & Bull, 1966). On various species of polyzoa.

Loxosomella obesa (Atkins, 1932) [Prenant & Bobin, 1956 : 66].

Described from Plymouth; also recorded from Anglesey; the Isle of Man (Eggleston, 1965); and Bergen (Nielsen, 1964*b*). On *Aphrodita aculeata*.

Loxosomella ornata Nielsen, 1964 [Nielsen, 1964*a* : 24].

In the tubes of *Thelepus cincinatus*, from the Skagerrak to the Öresund.

Loxosomella polita Nielsen, 1964 [Nielsen, 1964*a* : 22].

In tubes of *Petaloproctus tenuis* and *Nicomache lumbricalis* from the Kattegat and Öresund; Bergen (Nielsen, 1964*b*).

Loxosomella scaura Nielsen, 1964 [Nielsen, 1964*a* : 47].

On the setae of *Nephtys* spp., Skagerrak and Kattegat.

Loxosomella similis Nielsen, 1964 [Nielsen, 1964*a* : 20].

In tubes of *Nicomache trispinata* from the Kattegat; Bergen (Nielsen, 1964*b*).

Loxosomella teissieri (Bobin & Prenant, 1953) [Prenant & Bobin, 1956 : 53, as *Loxocalyx*].

On the sponge *Dysidea fragilis*, Roscoff. I follow Nielsen (1964*a*) in uniting *Loxocalyx* with *Loxosomella*.

Loxosomella varians Nielsen 1964 [Nielsen, 1964*a* : 49].

On *Nephtys* spp., Skagerrak to Öresund, very abundant; Bergen (Nielsen, 1964*b*).

4. SUMMARY

Each species described by Hincks in the "British Marine Polyzoa", together with any varieties, is listed beside its appropriate page number. The name now recommended or generally accepted for each is then given, with author and date of introduction. If Hincks' name embraced more than one species, this is indicated. Where the present nomenclature differs from that of Hincks, brief documentation is given. In addition, 127 species which have been recorded since 1880 in European waters between latitudes 46° and 62° N are listed, together with the references documenting their discovery in the British area and providing an illustrated description. These supplementary records comprise fifty-seven cheilostomes, eighteen ctenostomes, nine cyclostomes and forty-three entoprocts.

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6. ADDENDUM

Maturo & Schopf (1968), in a publication received since the type of the present paper was set, have given details of type material of American Polyzoa described by Verrill & Dawson. The new information about four of these species affects the nomenclature adopted in this list, and is summarized below:

(1) 291 *Hippothoa expansa* Dawson, 1859 [p. 224]. The species described by Hincks differs in a number of ways from Dawson's syntypes, and is to be regarded as a separate species needing a new name.

(2) *Dendrobeania elongata* (Nordgaard, 1906). [Additional species, p. 240.] Nordgaard's species is recognized as being identical with *Bugula decorata* Verrill, so that the correct name is *Dendrobeania decorata* (Verrill, 1879).

(3) *Erymophora gracilis* (Nichols, 1911). [Additional species, p. 240.] This species is recognized as identical with *Bugulella fragilis* Verrill (1879). As *B. fragilis* is the only valid genosyntype, it follows that *Erymophora* Hastings (1943) is a junior synonym of *Bugulella* Verrill. The correct name of the species is *Bugulella fragilis* Verrill, 1879.

(4) *Myriozoella plana* (Dawson, 1859). [Additional species, p. 241.] *Myriozoum crustaceum* Smitt (1868*b*) differs in several ways from *Lepralia plana* Dawson, and is to be regarded as a distinct species. The correct name for the present species, therefore, is *Myriozoella crustacea* (Smitt, 1868).

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THE CLUPEOID FISHES DESCRIBED BY BLOCH AND SCHNEIDER

By P. J. P. WHITEHEAD

INTRODUCTION

This is the fourth in a series of studies (Whitehead, Boeseman & Wheeler, 1966; Whitehead, 1966, 1967) dealing with a fundamental problem in the systematics of clupeoid fishes—the problem of poor original descriptions relating to material that has rarely been re-examined. The clupeoid species described by Bloch and by Schneider are particularly important because they provide some of the oldest names still in use and because the types have not been redescribed in the modern era of clupeoid systematics, that is to say since Regan's pioneering studies of some 40 years ago.

The Bloch & Schneider types have been in the Zoologisches Museum in Berlin for nearly 170 years, but damage during the 1939–45 war and subsequent curatorial difficulties in restoring the large collection to a workable state has led to the loss or misplacement of specimens. Thorough search produced 4 clupeoid types but one could not be found (*Clupea malabaricus*) and a neotype is recommended. Certain other specimens are commented on here since misidentifications have led to errors in the literature.

Marcus Elieser Bloch (1723–99) published about a dozen ichthyological papers, but his major work was a 12-volume compilation entitled *Allgemeine Naturgeschichte der Fische*, 1782–95 (which was made up of the 3 parts of his *Oeconomische Naturgeschichte der Fische Deutschlands*, 1782–85 and the 9 parts of his *Naturgeschichte der ausländischen Fische*, 1783–95; the 432 plates were numbered as a continuous series). A French translation of this work (by Laveau) appeared in 12 parts in 1785–88 and 1797, and a cheap edition by Castell in 10 volumes was published in 1801 in " Suites à Buffon " (volumes 32–41), with Bloch's plates copied and reduced by de Sève.

After Bloch's death, Johann Gottlob Schneider (1750–1822) completed his colleague's work by compiling a synopsis of all described species under the title *M. E. Blochii, . . . Systema Ichthyologiae, iconibus ex illustratum*, published in 1801. In this work Schneider marked with an asterisk those species represented by specimens in the Museum Blochiana. Those not marked were thus unavailable to Bloch and the description either follows earlier authors or must be attributed to Schneider (who often wrote " Schn. " after his additions to Bloch descriptions).

Bloch listed 12 species under the Linnaean genus *Clupea* (see Table 1). All but one are clupeoids (8 Clupeidae, 3 Engraulidae but 1 Megalopidae) and three were new species (*C. africana*, *C. nasus* and *C. malabaricus*). In addition to Bloch's 12 species, Schneider listed a further 10 and proposed a new clupeoid genus, *Gnathobolus* (= *Odontognathus* Lacepède). Of Schneider's additional species, 4 are not clupeoids

TABLE I

THE CLUPEOID FISHES OF BLOCH AND SCHNEIDER

Bl.	Page and volume number in *Oecon. Nat. Fische Deutsch.* or *Nat. ausl. Fische.*
Schn.	Page number in *Syst. Ichth. Blochii.*
Plate.	Plate numbers in Bloch's works (which were numbered consecutively).

(new names in **bold face**)

A. *CLUPEOID SPECIES*

	Bl.	Schn.	Plate	Identification
CHIROCENTRIDAE				
1. **Clupea dentex** Forssk.	—	428	—	*Chirocentrus dorab* (Forsskål, 1775)
CLUPEIDAE				
2. *Clupea harengus* L.	I 186	422	29 (1)	*Clupea harengus* Linnaeus, 1758
3. *Clupea sprattus* L.	I 206	423	29 (2)	*Sprattus sprattus* (Linnaeus, 1758)
4. *Clupea pilchardus*	IX 40	425	406	*Sardina pilchardus* (Walbaum, 1792)
5. *Clupea trissa*	IX 35	—	—	Figure = *Opisthonema oglinum*
(i.e. *thrissa* L.)	—	424	404	(Le Sueur, 1817), text composite (see p. 266)
6. *Clupea alosa* L.	I 209	432	30 (2)	*Alosa alosa* (Linnaeus, 1758)
7. *Clupea sinensis* L.	IX 38	424	405	*Hilsa kelee* (Cuvier, 1829)
8. **Clupea africana** Bloch	IX 45	425	407	*Ilisha africana* (Bloch, 1795)
9. **Clupea melastoma** Schn.	—	427	—	*Ilisha melastoma* (Schneider, 1801)
10. *Gnathobolus* [*mucronatus*] Lac.	—	556	—	*Odontognathus mucronatus* (Lacepède, 1801)
11. **Clupea nasus** Bloch	IX 116	426	429 (1)	*Nematalosa nasus* (Bloch, 1795)
ENGRAULIDAE				
12. *Clupea encrasicolus* L.	I 212	423	30 (2)	*Engraulis encrasicolus* (Linnaeus, 1758)
13. *Clupea atherinoides* L.	IX 46	427	408 (1)	*Pterengraulis atherinoides* (Linnaeus, 1766)
14. *Clupea baelama* Forssk.	—	429	—	*Thrissina baelama* (Forsskål, 1775)
15. **Clupea malabaricus** Bloch	IX 115	425	432	*Thryssa malabarica* (Bloch, 1795)
16. **Clupea mystax** Schn.	—	426	(pl. 83)	*Thryssa mystax* (Schneider, 1801)
17. *Clupea setirostris* Brouss.	—	428	—	*Thryssa setirostris* (Broussonet, 1782)
18. *Clupea mystus* L.	—	428	—	*Coilia mystus* (Linnaeus, 1758)

B. *NON-CLUPEOID SPECIES*

	Bl.	Schn.	Plate	Identification
ALBULIDAE				
19. **Clupea brasiliensis** Marc.	—	427	—	*Albula vulpes* (Linnaeus, 1758)

	Bl.	Schn.	Plate	Identification
MEGALOPIDAE				
20. **Clupea thrissoides** Schn.	—	424	—	*Megalops cyprinoides* (Broussonet 1782)
21. *Clupea cyprinoides* Brouss.	IX 32	—	403	*M. cyprinoides*
NOTOPTERIDAE				
22. **Clupea synura** Schn.	—	426	—	*Notopterus notopterus* (Pallas, 1769)
DOUBTFUL				
23. *Clupea brunnichii* Schn.	—	424	—	? (see p. 274)

(Table 1) and of the remainder (1 Chirocentridae, 2 Clupeidae and 4 Engraulidae) 2 were described as new (*C. melastoma* and *C. mystax*).

The older jars in Berlin usually bear small rectangular labels about 50 mm. long. The labels fall into 3 groups whose relative ages can be inferred from instances where a second or third label was pasted over an older one (as in the case of *Clupea melastoma*—see p. 270).

Type a label. Plain white paper, less than 25 mm. broad, without border, writing in flowing script. It is not certain if these date from Bloch (see under *Clupea melastoma*, p. 270).

Type b label. Thicker paper, about 25 × 50 mm., with characteristic printed border of 2 black lines thickened along the lower and right edges of the outer border (and reverse for inner border) to give inset effect. Species name, locality and " Bl. " are printed by hand in heavy Gothic script. Register numbers appear to have been added later. The labels are sometimes coloured green, blue, yellow, etc., possibly in accordance with geographical areas.

Type c label. Similar to the above but the outer border thick on all 4 sides and the inner border thin. Information on label in fine flowing script. A label bearing the name *Chatoessus* shows that these were in use after Cuvier's proposal of that name in 1829. Register numbers on these labels appear to be contemporary with the label. The labels are sometimes coloured.

Some of the jars also bear a small, square label (about 10 × 10 mm.) with a number written in heavy strokes as in type *b* labels. The numbers occasionally match the species numbers used by Bloch (or by Schneider) but this appears to be coincidence.

The specimens preserved in alcohol are in good condition although often rather flaccid. The dry specimens, of which many seem to have been lost, are in poor condition. The specimens are listed in a catalogue dated 1860; the entries were probably copied from an older catalogue which no longer exists.

ACKNOWLEDGEMENTS

I am indebted to Dr. Kurt Deckert for permission to examine the collection in Berlin and for facilities provided; Dr. Christine Karrer greatly assisted in the search for specimens and literature.

THE CLUPEOID FISHES OF BLOCH AND SCHNEIDER

CHIROCENTRIDAE

1. *Clupea dentex*

= *Chirocentrus dorab* (Forsskål, 1775)

Clupea dorab Forsskål, 1775, *Descript. Animal.* : xii, 72.
Clupea dentex Schneider, 1801, *Syst. Ichth. Bloch.* : 428 (Red Sea).

Schneider merely proposed a new name for Forsskål's species.

CLUPEIDAE

2. *Clupea harengus*

= *Clupea harengus* Linnaeus, 1758

Clupea harengus Linnaeus, 1758, *Syst. Nat.*, 10th ed. : 317; Bloch, 1782, *Oecon. Naturg. Fische Deutsch.*, **1** : 186, pl. 29 (1); Schneider, 1801, *Syst. Ichth. Bloch.* : 422.

3. *Clupea sprattus*

= *Sprattus sprattus* (Linnaeus, 1758)

Clupea sprattus Linnaeus, 1758, *Syst. Nat.*, 10th edition : 318; Bloch, 1782, *Oecon. Naturg. Fische Deutsch.*, **1** : 206, pl. 29 (2); Schneider, 1801, *Syst. Ichth. Bloch.* : 423.

4. *Clupea pilchardus*

= *Sardina pilchardus* (Walbaum, 1792)

Clupea pilchardus Walbaum, 1792, in Artedi, *Gen. Pisc.* : 38; Bloch, 1795, *Naturg. ausl. Fische*, **9** : 40, pl. 406; Schneider, 1801, *Syst. Ichth. Bloch.* : 425.

5. *Clupea trissa* (or *thrissa*)

(Pl. 1a)

= *Opisthonema oglinum* (Le Sueur, 1817)

[*Halex festucosus*—Plumier MS name on drawing, see below].
[*Clupea minor*, radio ultimo pinnae dorsalis longissimo—Brown, 1756, *Civil Nat. Hist. Jamaica* : 443].
[*Cailleu-Tassart des Antilles* Duhamel, 1772, *Traité Géneral Pêsches.*, **3** (2) : 548, pl. 31 (3)—on Barbotteau].
Clupea trissa Bloch, 1795, *Naturg. ausl. Fische*, **9** : 35 (emendation of *thrissa*).
Clupea thrissa (*non* Linnaeus, 1758) Bloch, *idem*, 1795, pl. 404; Schneider, 1801, *Syst. Ichth. Bloch.* : 424.
Megalops oglina Le Sueur, 1817, *J. Acad. nat. Sci. Philad.*, **1** : 359.

Bloch's plate 404 is a copy of a drawing by Father Plumier (see Plate 1b), almost certainly the one entitled *Halex festucosus* now in the Bibliothèque Centrale in Paris (MS. 24, pl. 4). Bloch based his description entirely on the drawing, which shows the Western Atlantic *Opisthonema oglinum*.

The name *thrissa* (*trissa*, *triza*, etc.) stems from the description of a Chinese gizzard shad (i.e. *Clupanodon thrissa*) by Osbeck (1757) which was first published as a valid name by Linnaeus (1758). Unfortunately Linnaeus and many subsequent authors included the Western Atlantic *Opisthonema* in their descriptions or synonymies of the Chinese *Clupanodon*. Thus Linnaeus (1758) not only made reference to Brown's *Clupea minor* from Jamaica, but also identified a specimen of *Opisthonema oglinum*, sent by Charles Blagden from Carolina, as *Clupea thrissa* (Günther, 1899—specimen in Linnean Society collection, London). Considerable confusion arose because "*thrissa*" was claimed as type of both the Chinese *Clupanodon* of Lacepède and the American *Opisthonema* of Gill, the filamentous last dorsal ray being a feature common to the two genera.

Although Bloch's description of *Clupea trissa* clearly refers to the American *Opisthonema oglinum*, Bloch mentioned the Chinese records of Osbeck and Linnaeus as well as the excellent description and figure of *Clupanodon thrissa* by Broussonet (1782).

6. *Clupea alosa*

= *Alosa alosa* (Linnaeus, 1758)

Clupea alosa Linnaeus, 1758, *Syst. Nat.*, 10th ed. : 318; Bloch, 1782, *Oecon. Naturg. Fische Deutsch.*, **1** : 209, pl. 30 (1); Schneider, 1801, *Syst. Ichth. Bloch.* : 423.

7. *Clupea sinensis*

(Pl. 1c)

= *Hilsa kelee* (Cuvier, 1829)

? *Clupea sinensis* Linnaeus, 1758, *Syst. Nat.*, 10th ed. : 319; Bloch, 1795, *Naturg. ausl. Fische*, **9** : 38, pl. 405; Schneider, 1801, *Syst. Ichth. Bloch.* : 424.
Clupea chinensis Cuvier, 1817, *Règne Animal*, 1st ed. : 174 (on Bloch—omitted from 2nd ed.).
Clupea kelee Cuvier, 1829, *Règne Animal*, 2nd ed., **2** : 320 (on *Keelee* of Russell).
Clupeonia blochii Valenciennes, 1847, *Hist. Nat. Poiss.*, **20** : 353 (on Bloch's *Clupea sinensis*).

SPECIMENS. A skin, right side only, with label on reverse "*Clupea sinensis*", mounted on stand on base of which is a label (without border) "*Clupea sinensis* Lin. M. Bl. Bl. t. 405" and a smaller label "98." pasted below. The specimen has the catalogue number 21893. It is probably the one sent from Tranquebar by the Rev. John.

Description. The specimen is in poor condition, but the following measurements were possible.

S.L. 161 mm.; tot. l. 205 mm.; body depth 69·3 mm.; head length 51·9 mm.; pectoral length 30·3 mm.; pre-dorsal distance 80·2 mm.; pre-pelvic distance 94·4 mm.

IDENTIFICATION. The notched upper jaw, striated maxilla, presence of fronto-parietal striae and deep body identify the fish as *Hilsa kelee* (diagnosis in Whitehead, 1965 : 132). The characteristic black spots along the flanks, retained in some preserved specimens of *H. kelee*, are absent and all black markings appear to be dirt.

The specimen was twice examined by Prof. Peters, first for Günther and then for Day. Day (1878 : 641) believed the specimen to be *Hilsa toli* (Valenciennes), but Günther (1868 : 446) identified it as *Hilsa ilisha* (Ham. Buch.); most of Günther's *ilisha* material was, however, *H. kelee* (Whitehead, 1965 : 145).

There is a second and smaller specimen of *Clupea sinensis* in the collections in Berlin. This fish, 93 mm. S.L. and 125 mm. tot. l., is preserved in alcohol. The jar bears a type *c* label (see Introduction, p. 265) " *Clupea sinensis* Bl.* Indischer Oz. 3846 A $\frac{3}{16}$ l.l. 50/D [?] " and beneath this a type *b* label " *C. sinensis* Lin. 3.4.15 Ind. Oc. 3846 Bl." The significance of the asterisk is not now known.

This juvenile fish has no striae along the maxilla, a barely developed cleithral lobe, few fronto-parietal striae, 18 + 13 scutes, pectoral fin tips just reaching to pelvic base, caudal lobes less than head length, the pseudobranch attenuated and with a groove below it, and an operculum twice as deep as broad. This clearly identifies it as *Hilsa ilisha*.

Bloch (in the Castel edition of 1801) stated that he received *Clupea sinensis* from the Rev. John of Tranquebar under the name *poiken* or *nannalai*, a fact not given in the original edition of 1795 (in which Bloch records Japan and Tranquebar, as well as American coasts, as localities.) Although the juvenile specimen mentioned above bears a type *b* label, it seems unlikely that such a small fish was used for Bloch's figure or description.

Bloch's figure of *Clupea sinensis* (pl. 405) formed the basis for *Clupeonia blochii* Valenciennes. Although the standard length of the larger specimen is 64 mm. shorter than that of the figure, Bloch's drawings were not necessarily life size (the pilchard is 12 inches long, for example) and the present specimen is quite likely model for the drawing and can be considered the type of *Clupeonia blochii*. According to Day (1878), Prof. Peters also believed this fish to have been the basis of the drawing.

Clupea sinensis Linnaeus has been discussed as a possible senior synonym of *Hilsa toli*, but no conclusion was reached (Whitehead, 1965 : 144). The Linnaean species might have been the same as Bloch's (i.e. *Hilsa kelee*) although Hong Kong appears to be at the limit of the range of that species (no record in the literature but four juveniles in British Museum collection). The name *sinensis* suffered various interpretations (e.g. Lacepède's *Clupanodon sinensis*—see Whitehead, 1967 : 57) and was finally abandoned until revived by Fowler (1941 : 631) as a senior synonym of *Hilsa toli*. The type is not in Uppsala (Lönnberg, 1896; Holm, 1957) nor in London (Günther, 1899) and in the absence of better evidence of its identity than the original description, the name *Clupea sinensis* Linnaeus is best rejected as a *nomen dubium*.

8. *Clupea africana*

(Pl. 2a)

= ***Ilisha africana*** (Bloch, 1795)

Clupea africana Bloch, 1795, *Naturg. ausl. Fische*, **9** : 45, pl. 407 (Accra; Br. St. 5, D 18, P 16, V 6, A 46); Schneider, 1801, *Syst. Ichth. Bloch.* : 425.

TYPE. A specimen in alcohol in a jar bearing a green type *b* label " *C. africana*. Bl. Aethiop. M. 3874 Bl. " to which the name *Pellona Iserti* V. has been added at a later date.

DESCRIPTION. *Holotype*, a fish of 154·2 mm. S.L. (193 mm. tot. l.), in fair condition but snout damaged, belly split below pectoral fin, back damaged behind head and scales shed, ZMB. 3874.

Br. St. 6, Diii 13, P i 12, V i 5 (or i 6), A iii 43, g.r. 23, scutes 26 + 7 (or 8).

In percentages of standard length: body depth 33·1, body width 5·2, head length 26·8; snout length 7·9, eye diameter 8·1, upper jaw length 13·2, lower jaw length 12·5; pectoral fin length 17·8 (damaged, estimated 19·1), pelvic fin length 3·0 (damaged, estimated 3·9), length of anal fin base 41·3; pre-dorsal distance 53·8, pre-pelvic distance 46·0, pre-anal distance 57·8.

Body strongly compressed, its width 5 times in depth, the latter greater than head length; belly keeled, scutes trenchant, especially behind pelvic fins. Snout a little shorter than eye diameter. Lower jaw strongly projecting with 3 (right) and 5 (left) conical teeth on either side of the symphysis. About 10 small teeth on each pre-maxilla. Two supra-maxillae (anterior one missing on right side), the posterior with ventral bulge and tapering posterior tip which just fails to reach tip of maxilla; the latter blunt posteriorly and with a series of fine teeth along ventral margin. No hypo-maxilla present.

Pseudobranch present, exposed, with 18 filaments the longest being ½ eye diameter. Gillrakers moderate, the longest ½ eye diameter, the corresponding gill filaments half that length. Dorsal surface of head with 2 prominent longitudinal ridges on each side, the outer one interrupted behind eye, and a third short ridge above the temporal foramen.

Dorsal fin origin nearer to snout than to caudal base by ⅓ eye diameter, in advance of vertical from anal origin by ¼ eye diameter. Pectoral tips reaching to beyond vertical from pelvic base; base of first ray on a level with lower border of eye. Pelvic base 1½ eye diameters in front of anal origin. The latter equidistant between eye centre and caudal base and below vertical from sixth branched dorsal ray.

COLOUR. Upper ⅕ of body brown, remainder silvery; no marks on body or fins.

IDENTIFICATION. This is the only member of the Pristigasterinae known from West Africa and the long anal fin and projecting lower jaw make it unmistakable. The types of the following nominal species have been examined and found to be conspecific (Whitehead, 1967 : 112).

Pellona gabonica Duméril, 1858
Pristigaster dolloi Boulenger, 1902
Ilisha melanota Derscheid, 1924

TYPE STATUS. The label on the jar (type *b*) suggests that this specimen was from the Museum Blochiana, although Schneider (1801 : 425) did not place an asterisk against it, possibly in error. Again, the locality given (Aethiopian Sea) is curious because Bloch (1795 : 45) specifically states Acara (i.e. Accra). But it seems preferable to regard these as errors and to recognize the specimen as the holotype of *Clupea africana* Bloch.

Valenciennes (1847 : 307) may have based his description of *Pellona iserti* on specimens but this is not clear from the description; there are no such specimens in

Paris (Whitehead, 1967 : 112). He cited Bloch's name and quoted Bloch's meristic figures but proposed a new name because of differences between his material (or drawing or notes by Dr. Isert) and Bloch's figure (profile of the back more convex but belly less so, etc.). Valenciennes' species is clearly the same as Bloch's, and since only a single West African species of *Ilisha* is known, no point would be served in providing a type for *Pellona iserti*.

9. *Clupea melastoma*

= *Ilisha melastoma* (Schneider, 1801)

Clupea melastoma Schneider, 1801, *Syst. Ichth. Bloch.* : 427 (Indian Ocean, near Coromandel; Br. St. 6, D15, P14, V6, A34).
Pellona micropus Valenciennes, 1847, *Hist. Nat. Poiss.*, **20** : 320.
Ilisha brachysoma Bleeker, 1852, *Verh. Bat. Gen.*, **24** : 22.

TYPE. A specimen in alcohol in a jar with a yellow type *c* label " *Pellona melastoma* Bl. Schn. Indisch. Oz 3842 Bloch ", beneath which is a type *b* label " *C. melastoma* Bl. S Ind. Oc. Bl. ", beneath which is yet a third label (type *a*) " *Clupea melastoma* (Kutta Wai Bl) Bl. " A very small square label on the jar is inscribed " 10 ".

DESCRIPTION. *Holotype*, a fish of 118·9 mm. S.L. (154·9 mm. tot. l.), caudal tips complete but tips of pelvics, pectorals and dorsal damaged, as also belly below pectorals, ZMB. 3842.

Br. St. 6, D iv 13 (last ray double), P i 14, V i 5, A ii 35, g.r. 23, scutes 8 [+ 2] 8 + 9.

In percentages of standard length: body depth 37·8, head length 28·2; snout length 6·8, eye diameter 10·0, length of upper jaw 13·6, length of lower jaw 14·0; pectoral fin length 18·7, pelvic fin length (tip broken) 4·9, length of anal base 33·8; pre-dorsal distance 49·2, pre-pelvic distance 48·1, pre-anal distance 65·1.

Body strongly compressed, deeper than head length, belly sharply keeled. Snout a little shorter than eye diameter. Lower jaw strongly projecting, about 5 small conical teeth on either side of symphysis. Small granular teeth present on tongue. Pre-maxilla with a single row of small conical teeth giving way towards the centre of the upper jaw to a row of small papillae. Two supra-maxillae, the anterior 5·7 mm. long with narrow anterior shaft, the posterior with expanded portion 6·3 mm. long, with ventral bulge but tapering posteriorly to reach tip of maxilla (which extends to vertical from anterior margin of pupil); maxilla with minute teeth along lower edge. No hypo-maxilla.

Pseudobranch present, exposed, with 21 filaments the organ about ½ eye diameter in both length and breadth. Dorsal surface of head with a continuous ridge on each side flanked by a second ridge (discontinuous behind eyes) and two smaller ridges on parietal region.

Dorsal origin nearer to snout than to caudal base by ¼ eye diameter, behind vertical from pelvic base by ¾ eye diameter. Pectoral tips just reaching to pelvic base. The latter slightly nearer to pectoral base than to anal origin; no axillary scale. Anal origin under last dorsal ray.

Scales with 2 (anterior) to 4 (posterior) continuous vertical striae and 6 striae interrupted (anterior) or overlapping (posterior) in front of this; posterior margin of scale slightly crenulated and bearing fine, short horizontal striae.

IDENTIFICATION. Norman (1923), Fowler (1941) and Whitehead, Boeseman & Wheeler (1966 : 92) believed that Schneider's *Clupea melastoma* was a species of *Pellona* (i.e. *Pellona ditchela* Valenciennes), chiefly because of the low anal count (34 *fide* Schneider; 33–37 in *Pellona* and 37–52 in species of *Ilisha*). Schneider's statement that " *margine ossium maxillarum ensiformium anteriore toto crenulato* " was taken as further evidence for *Pellona* since it suggested the toothed hypomaxilla present in *Pellona* but absent in *Ilisha*. In the list of corrigenda, however, Schneider substituted *labialum* for *maxillarum*, and the resemblance to *Pellona* is further diminished by the higher anal count found in the specimen (37 not 34).

The identity of *Clupea melastoma* is problematical. In the key given by Whitehead *et alii* (1966 : 93) it lies between the deep-bodied *Ilisha brachysoma* (Bleeker) and the more slender *I. megaloptera* (Swainson). So also does the holotype of *Ilisha micropus* (Valenciennes) (Whitehead, 1967 : 116). These 3 nominal species may merely represent growth forms of a single widespread and variable species, in which case Schneider's *Clupea melastoma* should be included.

The name *melastoma* has not been used for over 50 years as a senior synonym and under Rule 23 (b) it should be rejected as a *nomen oblitum*. This is unfortunate because the next oldest name, Swainson's *megaloptera*, lacks a type and the description is poor. Use of the name *melastoma* would not conflict greatly with usuage and application will be made to retain it.

10. ***Gnathobolus* [*mucronatus*]**

(Pl. 2b)

= ***Odontognathus mucronatus*** (Lacepède, 1800)

Odontognathus mucronatus Lacepède, 1800, *Hist. Nat. Poiss.*, **2** : 220, 221, pl. 7 (2).
Gnathobolus [*mucronatus* inferred] Schneider, 1801, *Syst. Ichth. Bloch.* : 556.

Valenciennes (1848 : 87), in a particularly uncharitable passage, pointed out that had Lacepède not been so dominated by his own ideas of systematics and had he consulted his material instead of following Gmelin, he would have discovered that the curious toothed " horns " curving forward on either side of the mouth of his *Odontognathus mucronatus* were nothing else but the maxillae bent forwards. Schneider (1801), with only Lacepède's description and bizarre figure by de Sève (see Pl. 2b), recognized the " horns " as pieces of the upper jaw and proposed what he felt to be a more appropriate name (*Gnathobolus*). Cuvier (1829 : 321) acknowledged that the jaw position was an artifact, but continued to use the name *Gnathobolus*, as also did Valenciennes (*loc. cit.*).

11. *Clupea nasus*

(Pl. 2c)

= ***Nematalosa nasus*** (Bloch, 1795)

Clupea nasus Bloch, 1795, *Naturg. ausl. Fische*, **9** : 116, pl. 429 (1) (Tranquebar; Br. St. 4, D 16, P 13, V 6, A 20); Schneider, 1801, *Syst. Ichth. Bloch.* : 426.

TYPE. A specimen in alcohol in a jar with a type *c* label " *Chatoessus nasus* Bl. Indisch. Oc. 3898 Bloch." and a small square label " 12 ".

DESCRIPTION. *Holotype*, a fish of 110·0 mm. S.L. (147·1 mm. tot. l.), in fair condition, pelvic tips broken and tenth post-pelvic scute damaged, ZMB. 3898. Probably sent by the Rev. John of Tranquebar.

Br. St. 6, D iv 14, P i 15, V i 7, A iii 20, g.r. (numerous), scutes 17 + 12.

In percentages of standard length: body depth 38·3, head length 26·8; snout length 6·3, eye diameter 8·0, upper jaw length 8·3, lower jaw length 9·7; pectoral fin length 22·4, pelvic fin length 10·3 (damaged, 10·9 estimated), dorsal filament length 36·6, length of anal base 22·1; pre-dorsal distance 46·4, pre-pelvic distance 46·6, pre-anal distance 72·0.

Body compressed, belly keeled, especially behind pelvic base, body depth greater than head length. Snout shorter than eye diameter. Lower jaw inferior, edge of dentary flared outwards. Upper jaw short, maxilla reaching to vertical from anterior pupil border, hind end of maxilla rounded; a single (posterior) supra-maxilla with short anterior shaft, curving downwards posteriorly. No teeth in jaws.

Pseudobranch present, exposed, with 22 filaments, the base of the organ ridged with a small groove below. Gillrakers fine, short, about ½ diameter of pupil, corresponding gill filaments twice as long, the anterior and posterior hemibranchs equal. Cleithral lobe present but small. Lower edge of second suborbital in contact with upper margin of pre-operculum and reaching forward to articulation of lower jaw before rising at an angle of about 20° to the vertical to reach a point beneath the anterior pupil border.

Dorsal fin with last ray filamentous, its length almost equal to body depth, dorsal origin nearer to snout than to caudal base by 1¾ eye diameter and before vertical from pelvic base by ⅛ eye diameter. Pectoral tips just reaching beyond pelvic base. Pelvic base below 2nd unbranched dorsal ray, nearer to pectoral base than to anal origin by ⅔ eye diameter. Anal origin nearer to pelvic base than to caudal base by ¾ eye diameter.

Scales (about 45 in lateral series) with one continuous and 0 (anterior) to 3 (posterior) interrupted striae, the scale border slightly crenulated and bearing short horizontal striae.

IDENTIFICATION. *Nematalosa nasus* is distinguished from other members of this genus by the shape of the second suborbital (Whitehead, 1962). In other species the lower edge of this bone does not reach forward as far as the lower jaw articulation before rising at an angle of 45°, leaving an exposed trapezoidal space on the cheek (Text-fig. 1a). In *N. nasus* the lower edge of the 2nd suborbital reaches the lower jaw articulation and then rises quite steeply (20° in the type, but often almost vertical), leaving little of the cheek exposed (Text-fig. 1b). The species is otherwise very similar to *N. come* (Richardson).

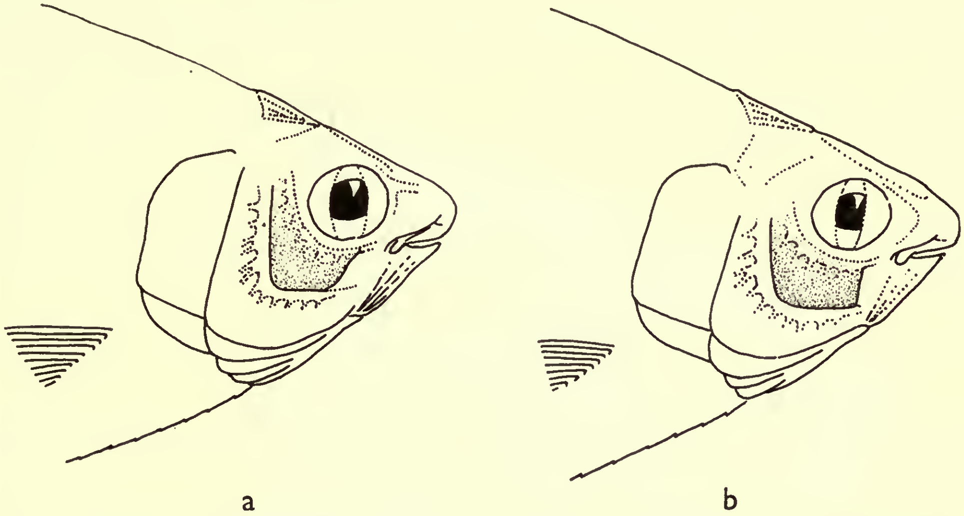

FIG. 1. Shape of 2nd sub-orbital (stippled) in species of *Nematalosa*. a. *Nematalosa come*, 128 mm. S.L., BMNH. 1844.2.21.69. b. *Nematalosa nasus*, 135 mm. S.L., BMNH. 1881.2.7.1880.

ENGRAULIDAE

12. *Clupea encrasicolus*

= *Engraulis encrasicolus* (Linnaeus, 1758)

Clupea encrasicolus Linnaeus, 1758, *Syst. Nat.*, 10th ed. : 318; Bloch, 1782, *Oeconom. Naturg. Fische Deutsch.*, **1** : 212, pl. 30 (2).
Clupea encrasicholus : Schneider, 1801, *Syst. Ichth. Bloch.* : 423.

Variations in the spelling of the species name still persist. Linnaeus (1735) first used *encrasicholus*, but the spelling in the 10th edition is definitive.

13. *Clupea atherinoides*

(Pl. 3a)

= *Pterengraulis atherinoides* (Linnaeus, 1766)

Clupea atherinoides Linnaeus, 1766, *Syst. Nat.*, 12th ed. : 523 (Surinam); Bloch, 1795, *Naturg. ausl. Fische*, **9** : 46, pl. 408 (1) (Surinam; Br. St. 12, D 11, P 14, V 8, A 35); Schneider, 1801, *Syst. Ichth. Bloch.* : 427.

SPECIMEN. A specimen in alcohol, 141·1 mm. S.L. (174·5 mm. tot. l.), in a jar bearing a green label " *Engraulis atherinoides* L. Surinam 3838 Bloch ". The fish is in fair condition, rather soft, the silver lateral stripe visible but the body darkened and the scales black.

IDENTIFICATION. The specimen is clearly the South American *P. atherinoides* as described and figured by Hildebrand (1964); Bloch's description and figure may well have been based on the present specimen. Bloch, however, believed the Mediterranean *Clupea maxilla superiore longiore, fascia laterali argentea* of Brunnich (1768 : 101) to be this species and also identified a Tranquebar specimen as *Clupea atherinoides*. The latter was most likely *Stolephorus indicus* (van Hasselt), while the former resembles *Engraulis encrasicolus* (the only Mediterranean anchovy species) except in its high anal count of 24 (about 17–19 in *E. encrasicolus*, including the three small unbranched rays) and low branchiostegal count (8, cf. 12). For this Brunnich species Schneider (1801 : 424) proposed the name *Clupea brunnichii*, but it cannot be positively identified with any known Adriatic clupeid (*Alosa*, *Sprattus*, *Sardina* and *Sardinella* have rather short maxillae quite unlike *Engraulis*, while an anal count of 24 would be exceptional even in *Alosa*).

14. *Clupea baelama*

= *Thrissina baelama* (Forsskål, 1775)

Clupea baelama Forsskål, 1775, *Descript. Animal.* : 72 (Djidda); Schneider, 1801, *Syst. Ichth. Bloch.* : 429.

Bloch ignored this Forsskål species although he was well aware of Forsskål's work.

15. *Clupea malabaricus*

(Pl. 3b)

= *Thryssa malabarica* (Bloch, 1795)

Clupea malabaricus Bloch, 1795, *Naturg. ausl. Fische*, **9** : 115, pl. 432 (Tranquebar; Br. St. 8, D 8, P 14, V 7, A 38); Schneider, 1801, *Syst. Ichth. Bloch.* : 425.

TYPE. Despite intensive search, no Bloch specimen of this species could be found, either in alcohol or in the dry collection. The genus *Thryssa* requires revision and the provision of types for those nominal species that have hitherto been known only by poor original descriptions would help to remove a great deal of existing confusion. A specimen has, therefore, been chosen which can stand as putative neotype pending a full revision.

DESCRIPTION. *Putative neotype*, a ripe female of 158·2 mm. S.L. (197 mm. tot. l.) in good condition except belly slit on left side, *ex* Madras (Day collection), BMNH. 1868.10.25.27.

Br. St. 12, D I iii 11, P i 12, V i 6, A iii 36, g.r. 14 + 17, scutes 15 + 9.

In percentages of standard length: body depth 36·5, width of body 10·0, head length 24·9; snout length 5·1, eye diameter 6·0, length of upper jaw 24·7, length of lower jaw 17·6; dorsal fin height 21·3, pectoral fin length 18·8, pelvic fin length 9·2, height of anal fin (greatest) 12·2, length of anal fin base 33·0; pre-dorsal distance 51·7, pre-pelvic distance 43·9, pre-anal distance 65·8; depth of caudal peduncle 10·7.

Body compressed, its width 3·6 times in its depth, head length less than body depth. Snout a little smaller than eye diameter. Mouth at an angle of about 15°

to the horizontal. Lower jaw with a single series of close-set teeth. Upper jaw with a single series of small teeth along entire edge; maxilla reaching gill opening and projecting 0·9 mm. beyond (10·3 mm. behind end of posterior supra-maxilla); the latter with slender anterior shaft expanding posteriorly to form a rounded ventral lobe 3·1 mm. long; anterior supra-maxilla round, minute (1·15 mm. long) (Text-fig. 2).

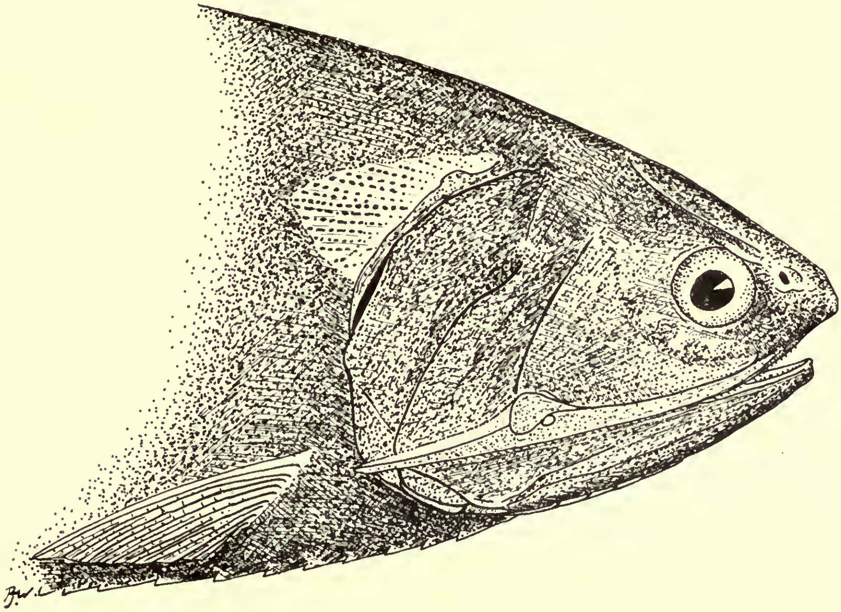

FIG. 2. *Thryssa malabarica*, 158·2 mm. S.L., putative neotype, BMNH. 1868.10.25.27. Maxilla extends 0·9 mm. beyond gill opening.

Pseudobranch present, concealed. Gillrakers short, the longest just over eye diameter, the corresponding gill filaments a little shorter (5·3 mm.); gillraker serrae not clumped; 6 short gillrakers present on posterior face of 3rd epibranchial. Vomer with two clumps of teeth (left 1, right 3); a line of granular teeth on edges of palatine and endo-pterygoid and patch of granular teeth on ecto-pterygoid. Sterno-hyoideus muscle reaching forward to beyond hind border of branchiostegal membrane. Posterior frontal fontanelles present, triangular. Venulose flap of skin behind operculum bearing about sixteen horizontal rows of dark brown dots.

Dorsal preceded by scute-like plate bearing a small spine, base of fin invested in low scaly sheath; dorsal origin about equidistant between snout and caudal base and above vertical from pelvic tips. Pectoral tips reaching to pelvic base; axillary scale present, just over $\frac{1}{2}$ length of fin. Pelvic base nearer to pectoral base than to anal origin by just over 1 pupil diameter; axillary scale present, a little more than half length of fin. Anal origin $\frac{3}{4}$ pupil diameter behind vertical from last dorsal ray, nearer to caudal base than to pectoral base by $\frac{3}{4}$ pupil diameter; fin covered to half its height by scaly sheath.

Scales with exposed portion bearing reticulated striae; unexposed portion with up to 8 vertical striae, the anterior striae becoming interrupted in the centre of the scale in the more posterior scales.

COLOUR. Upper $\frac{1}{3}$ of body brown, remainder silver, fins yellowish. Dark brown speckled pigmentation on pectoral fins, maxilla (except second supra-maxilla, which shows up white), margin of anal fin and venulose humeral region (a similar but much more intense pattern of pigmentation was described for Arabian Sea specimens (Whitehead, 1968) but in addition to the areas mentioned the dark pigments also occurred on the last unbranched dorsal and anal rays and on the margins of these fins and also on the caudal margin).

IDENTIFICATION. The most recent key to the species of *Thryssa* (Whitehead, 1968) makes a major separation of species on the length of the maxilla, i.e. reaching to gill opening, to just beyond, to pectoral base, to pectoral tip or beyond. But species with a short maxilla failing to reach the pectoral base may yet prove to be mere ontogenetic forms of the long maxilla group (see below under *Clupea mystax*). For *Clupea malabaricus*, Bloch's figure shows the maxilla just reaching the gill opening (see Pl. 3b) whereas in the specimen selected here the maxilla projects 0·9 mm. beyond. The difference is small and in fact is very much less than is found between individuals of other species (e.g. *T. dussumieri* and *T. vitrirostris*—Whitehead, 1968). Closely related to *T. malabarica* is *T. kempii* (Chaudhuri) of Lake Chilka in which the maxilla projects beyond the gill opening and about half-way to the pectoral base (photograph of holotype No. F. 8782/1 in the collection of the Zoological Survey of India kindly sent by Mr. M. Babu Rao). This species may prove to be *T. malabarica*.

16. *Clupea mystax*

(Pl. 3c)

= ***Thryssa mystax*** (Schneider, 1801)

Clupea mystax Schneider, 1801, *Syst. Ichth. Bloch.* : 426, pl. 83 (Malabar: Br. St. 5, D14, P14, V5, A34—the Br. St. clearly an error, as also the pelvic count).

TYPE. A fish preserved in alcohol in a jar bearing a type *b* label " *C. mystus* Lin. Ind. Oc. 3884 Bl. " and a small square label " 16 ", matching an entry in the register " *Engraulis mystus* L. Ind. Ocean Bloch. " Schneider (1801 : 426) did not indicate a Bloch specimen (by means of an asterisk) for this species although one is noted for *Clupea mystus* (a Linnaean species of *Coilia*—see Whitehead, 1967 : 141). The present specimen so closely matches Schneider's figure, however, that it must be presumed the type.

DESCRIPTION. *Holotype*, a fish of 134·7 mm. S.L. (160·7 mm. tot. l. but caudal tips damaged, estimated *ca.* 165 mm.), in poor condition, especially broken caudal tips, belly (split behind pectoral), right maxilla (tip loose) and loss of scales, *ex* Malabar, ZMB. 3884.

Br. St. 13, D I iii 12, P i 12, V i 6, A iii 33, g.r. 11 + 14, scutes 17 + 10.

In percentages of standard length: body depth 26·4, width of body 8·1, head length 25·7; snout length 4·9, eye diameter 5·9, length of upper jaw 30·4, length of lower jaw 19·6; length of pectoral fin 17·7, length of pelvic fin 8·8, length of anal base 30·2; pre-dorsal distance 53·0, pre-pectoral distance 27·2, pre-pelvic distance 41·8, pre-anal distance 63·4.

Body compressed, its width $3\frac{1}{3}$ times in its depth, belly sharply keeled, head length about equal to depth. Snout a little shorter than eye diameter. Lower jaw inferior, with a single series of fine conical teeth. Mouth slightly oblique, set at 15–20° from the horizontal. Upper jaw long and entirely toothed, maxilla projecting 3·7 mm. beyond pectoral base and 14·9 mm. beyond second supra-maxilla; the latter with slender anterior shaft followed by an expanded portion 2·8 mm. long and about as deep; anterior supra-maxilla present, 1 mm. long.

Pseudobranch present, concealed. Gillrakers short, the longest $\frac{2}{3}$ eye diameter, the corresponding gill filaments $\frac{1}{2}$ eye diameter; gillraker serrae not clumped; 7 small gillrakers on posterior face of 3rd epibranchial. Sterno-hyoideus muscle reaching forward to beyond hind border of branchiostegal membrane. Posterior frontal fontanelles present, triangular, 3·2 mm. long.

Dorsal preceded by small scute-like plate bearing a spine, base of fin invested in low scaly sheath; dorsal origin nearer to snout than to caudal base by $\frac{1}{2}$ eye diameter, behind vertical from pelvic base by $1\frac{3}{4}$ eye diameters. Pectoral tip projecting 3·8 mm. beyond pelvic base; axillary scale present, half length of fin. Pelvic base nearer to pectoral base than to anal origin by $1\frac{3}{4}$ eye diameters; axillary scale present, almost equal to fin length. Anal origin nearer to pectoral base than to caudal base by $\frac{1}{4}$ eye diameter; base of fin invested in low scaly sheath.

Scales with unexposed portion bearing 1 large and about 6 finer and more irregular striae the most anterior of which sometimes fail to meet in the centre of the scale; exposed portion becoming reticulated posteriorly.

IDENTIFICATION. According to the most recent key (Whitehead, 1968), *Thryssa mystax* most closely resembles *T. purava* (Ham. Buch.) but differs in having a lower anal count (35–41; cf. 43–49), a higher number of pre-pelvic scutes (17–19; cf. 14–17) and a less oblique mouth. Schneider's description is poor, but his figure (shown here, Pl. 3c) is adequate except that the maxilla is shown projecting too far beyond the pectoral base, the anal base is slightly too long and the origins of the dorsal, pelvic and anal fins are too advanced.

Elsewhere (Whitehead, 1966 : 43) it was suggested that maxilla length may vary with size of fish and that larger fishes with shorter maxillae (*C. hamiltonii* of authors) may be *C. mystax*.

17. *Clupea setirostris*

= *Thryssa setirostris* (Broussonet, 1782)

Clupea setirostris Broussonet, 1782, *Ichthyologia*, 1 : no pagination (Tanna I., Pacific).
Clupea setirostris: Schneider, 1801, *Syst. Ichth. Bloch.* : 428.

This Broussonet species is not mentioned by Bloch, but Schneider cited the original description and quoted the then MS name of J. R. Forster, *Clupea mystacina* (published some 40 years after Forster's death by Lichtenstein, 1844). The very long maxilla in this species, to beyond pelvic base, makes *T. setirostris* unmistakable.

18. *Clupea mystus*
= *Coilia mystus* (Linnaeus, 1758)

Clupea mystus Linnaeus, 1758, *Syst. Nat.*, 10th ed. : 319; Schneider, 1801, *Syst. Ichth. Bloch.* : 428.

This was another species not included by Bloch. The synonymy of *C. mystus* has been discussed recently (Whitehead, 1967 : 149).

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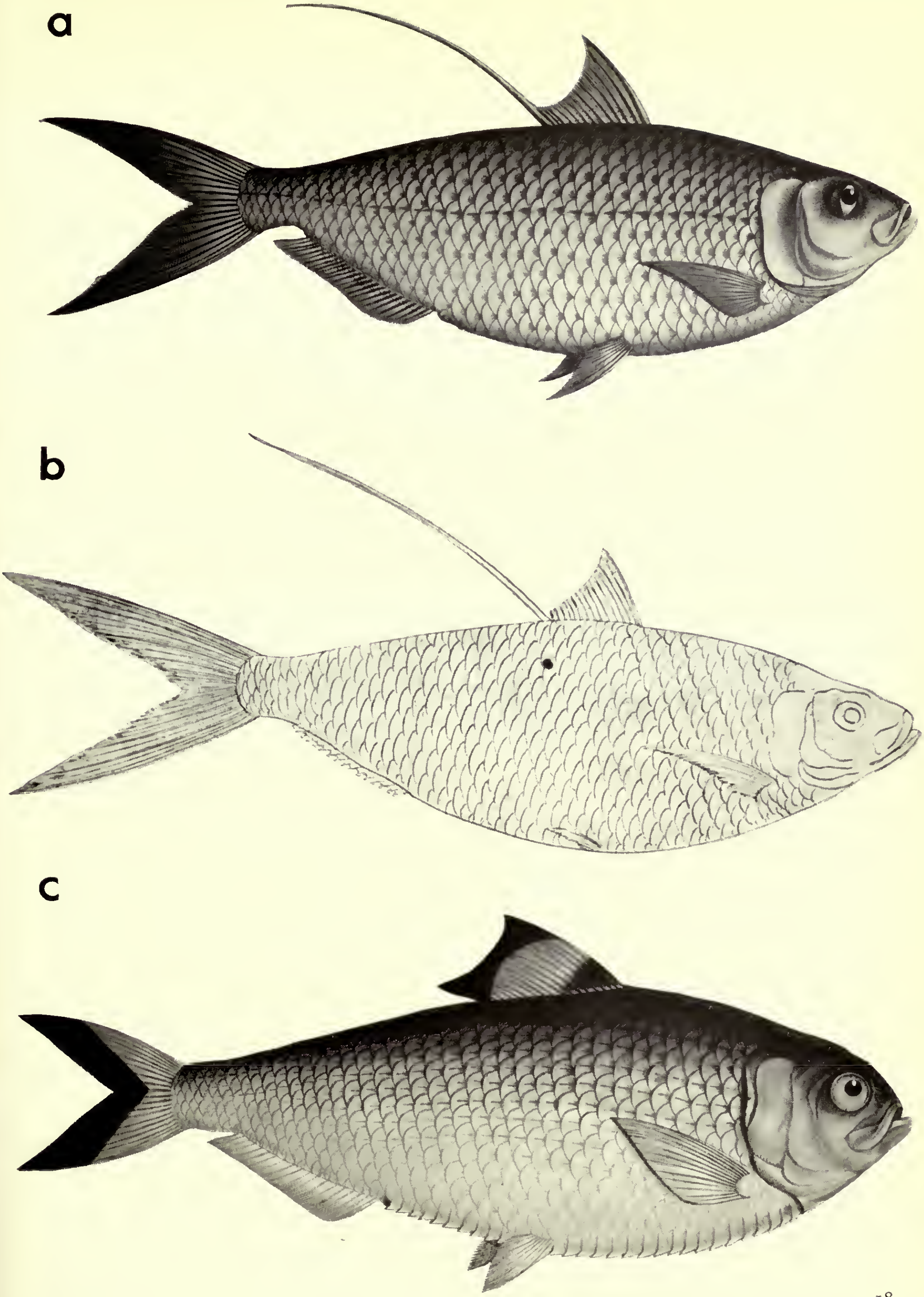
PLATE 1

a. *Clupea thrissa* from Bloch, pl. 404 (= *Opisthonema oglinum*—see p. 266).

b. " Halex festucosus ". Plumier drawing on which the Bloch figure was based—see p. 266 (= *Opisthonema oglinum*).

c. *Clupea sinensis* from Bloch, pl. 405 (= *Hilsa kelee*—see p. 267).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b
c

PLATE 2

a. *Clupea africana* from Bloch, pl. 407 (= *Ilisha africana*—see p. 268).
b. "Odontognathe aiguillonne" from Lacepède, vol. 2, pl. 7 (2), opp. p. 182 (= *Odontognathus mucronatus*—see p. 271).
c. *Clupea nasus* from Bloch, pl. 429 (= *Nematalosa nasus*—see p. 272).

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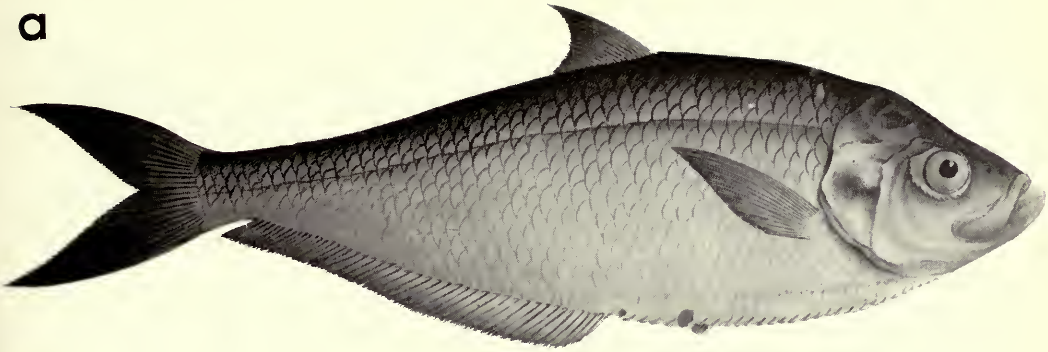

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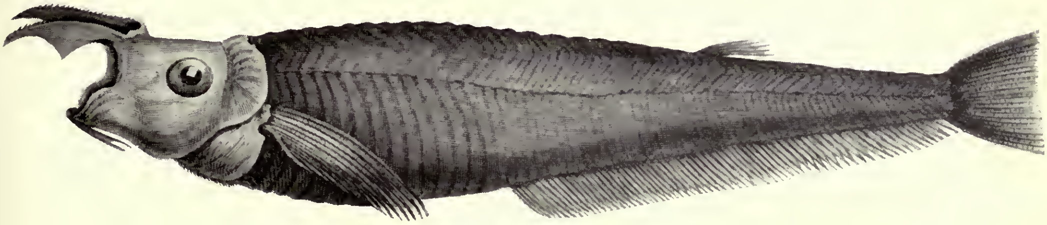

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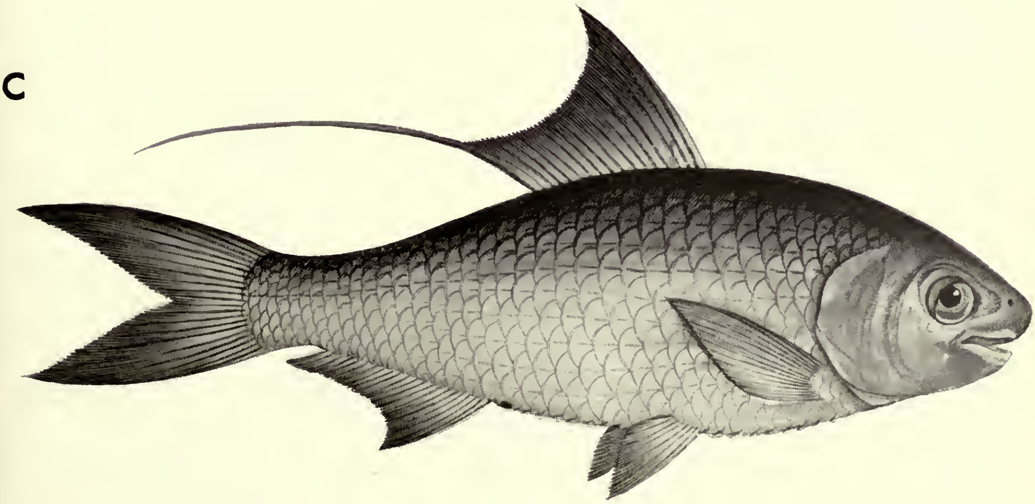

PLATE 3

a. *Clupea atherinoides* from Bloch, pl. 408 (1) (= *Pterengraulis atherinoides*—see p. 273).
b. *Clupea malabaricus* from Bloch, pl. 432 (= *Thryssa malabaricus*—see p. 274).
c. *Clupea mystax* from Schneider, pl. 83 (= *Thryssa mystax*—see p. 276).

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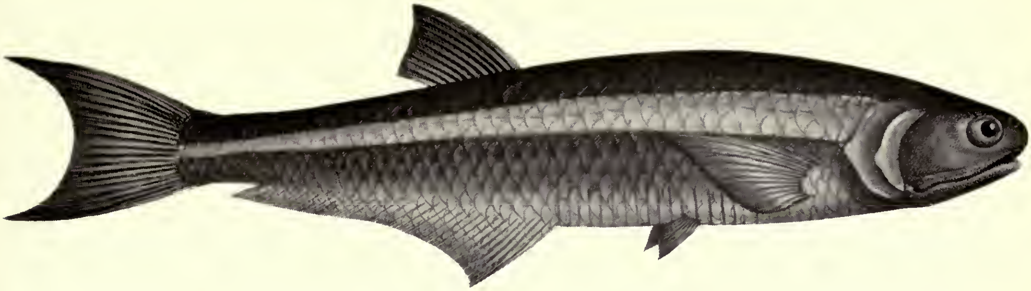

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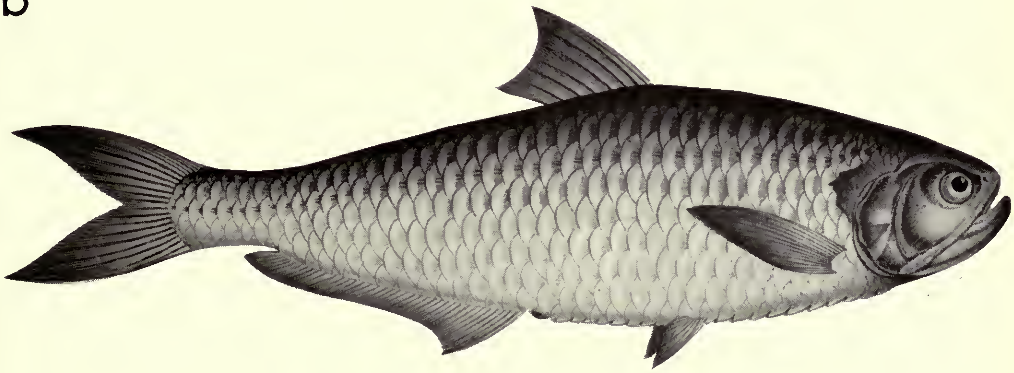

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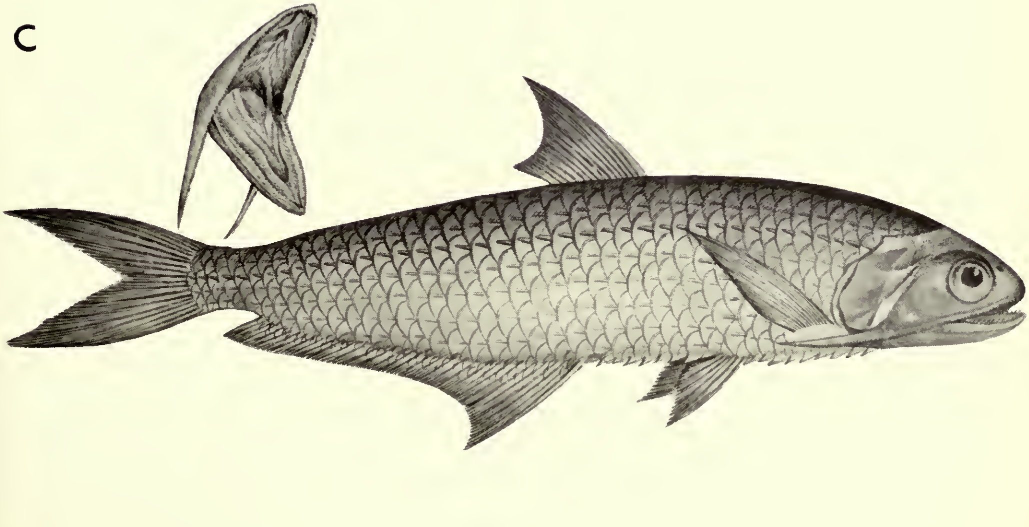

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BRITISH MUSEUM
6 MAY 1969
NATURAL HISTORY

MICHAEL D. B. BURT

BULLETIN OF
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ZOOLOGY Vol. 17. No. 8
LONDON : 1969

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Pp. 281–346; 60 Text- figures

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By MICHAEL D. B. BURT

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ABSTRACT

Twenty seven species of cestodes, collected from 20 species of birds in Borneo, are identified and described in the following order:

Paronia bocki Schmelz; *Raillietina echinobothrida* (Megnin); *R. johri* Ortlepp; *R. parviuncinata* Meggitt et Saw; *R. sequens* Tub. et Masil.; *R. allomyodes* Kótlan; *Raillietina* sp.; *R. siamensis* Schmelz; *Hymenolepis mahonae* nom. nov.; *Hymenolepis* sp.; *Fimbriaria fasciolaris* (Pallas); *Paricterotaenia burti* Sandeman; *Dilepis ardeolae* Singh; *Liga facile* (Meggitt); *Anomotaenia depressa* (Siebold); *A. nymphaea* (Schrank); *A. tringae* (Burt); *Parvitaenia* sp.; *Vitta rustica* (Neslobinsky); Dilepid sp.; *Kowalewskiella susanae* sp. nov.; *Ascometra* sp.; *Notopentorchis collocaliae* Burt; *Gyrocoelia perversa* Fuhrmann; Acoleid spp. (3).

Of these, two are new species, one is recorded from Asia for the first time, and the synonymy and taxonomy of each species is discussed. The descriptions are as complete as the material allowed and are supported by 60 text figures and 12 tables.

INTRODUCTION

The following cestodes form part of a collection of parasites collected from vertebrates by Dr. Robert E. Kuntz, United States Navy Medical Corps, in Borneo and sent to Dr. T. W. M. Cameron, Institute of Parasitology, Macdonald College, for identification. The species described are listed in systematic order. There are several new host-records and two new species are described. All drawings were made with the aid of a Wild drawing tube. Whole mounts were stained either in acetic acid alum-carmine or in Ehrlich's haematoxylin. Horizontal sections cut at 15 μ, and transverse sections cut at 5–10 μ, were stained in Ehrlich's haematoxylin and counterstained in eosin. Examination of rostellar hooks, sucker spines, and oncosphere hooks was facilitated by using Berlese fluid. Material prepared as whole mounts has been deposited in the collections of the British Museum (Natural History).

HOST LIST

APODIFORMES	
Apus affinis (J. E. Gray)	*Anomotaenia depressa* (Siebold, 1836)
	Notopentorchis collocaliae Burt, 1938
ANSERIFORMES	
Anas boschas domestica L.	*Fimbriaria fasciolaris* (Pallas, 1781)
CHARADRIIFORMES	
Actitis hypoleucos (L.)	*Liga facile* (Meggitt, 1927)
Charadrius leschenaultii Lesson	*Gyrocoelia perversa* Fuhrmann, 1899
	Paricterotaenia burti Sandeman, 1959
	Raillietina (*Paroniella*) *siamensis* Schmelz, 1941 (?)
	Species 1
	Species 2
	Species 3
Numenius phaeopus (L.)	*Anomotaenia nymphaea* (Schrank, 1790)
Tringa glareola L.	*Anomotaenia tringae* (Burt, 1940)
	Kowalewskiella susanae n. sp.
	Raillietina (*Raillietina*) *johri* Ortlepp, 1938 (?)
CICONIIFORMES	
Butorides striatus (L.)	*Dilepis ardeolae* Singh, 1952 (?)
	Parvitaenia sp.
COLUMBIFORMES	
Columba livia domestica L.	*Raillietina* (*Raillietina*) *sequens* Tubangui et Masiluñgan, 1937
Treron curvirostra (Gmelin)	*Raillietina* (*Raillietina*) sp.
Treron vernans (L.)	*Raillietina* (*Raillietina*) *allomyodes* Kótlan, 1921
	Raillietina (*Raillietina*) *johri* Ortlepp, 1938
Streptopelia chinensis (Scopoli)	*Raillietina* (*Raillietina*) *sequens* Tubangui et Masiluñgan, 1937
CUCULIFORMES	
Cacomantis merulinus (Scopoli)	Dilepididae
**Centropus toulou* (P.L.S. Müller)	*Ascometra* sp.

GALLIFORMES	
Gallus gallus (L.) *dom.*	*Raillietina* (*Raillietina*) *echinobothrida* (Megnin, 1881) *Raillietina* (*Raillietina*) *parviuncinata* Meggitt et Saw, 1924
PASSERIFORMES	
Aegithina tiphia (L.)	*Hymenolepis mahonae* nom. nov. *Raillietina* (*Raillietina*) *sequens* Tubangui et Masiluñgan, 1937
Anthreptes malacensis (Scopoli)	*Hymenolepis* sp.
Hirundo rustica L.	*Vitta rustica* (Neslobinsky, 1911)
Nectarinia calcostetha Jardine	*Hymenolepis* sp.
PICIFORMES	
Megalaima chrysopogon (Temminck)	*Paronia bocki* Schmelz, 1941 *Raillietina* (*Paroniella*) *siamensis* Schmelz, 1941
Meiglyptes tukki (Lesson)	*Raillietina* (*Paroniella*) *siamensis* Schmelz, 1941

* *Centropus toulou* (P. L. S. Müller) is not recorded from Borneo (Smythies: *The Birds of Borneo*, 1960) *C. t. toulou* (P. L. S. Müller) is found in Madagascar, *C. t. insularis* Ridgway is confined to Aldabra Is. and *C. t. assumptionis* confined to Assumption Is. The Bornean Coucals are the Common Coucal, *Centropus sinensis* (Stephens), the Lesser Coucal *C. bengalensis* (Gmelin) which is also common, and the rare Short-toed Coucal, *C. rectunguis* Strickland, a rare bird known from four specimens.

MORPHOLOGICAL DESCRIPTIONS

Family **ANOPLOCEPHALIDAE** Cholodkovsky, 1902

Genus ***PARONIA*** Diamare, 1900

Paronia bocki Schmelz, 1941

(Text-figs. 1–3)

HOST: *Megalaima chrysopogon* 8891*.

Only fragments of what appears to be one, incomplete worm are present and these total about 80 mm. in length. The maximum breadth is 2 mm. The proglottides are all broader than long with a tendency, in the more gravid proglottides, to become square.

The scolex is missing.

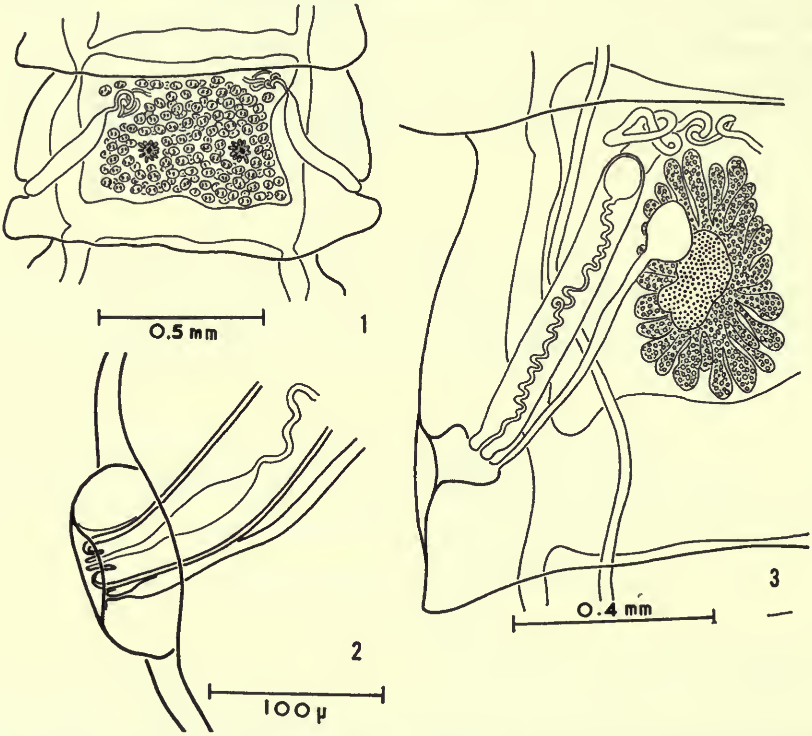
The testes are numerous (Text-fig. 1) and develop before the ovaries. Over 150 testes were seen in one proglottis, but they are difficult to count accurately owing to the displacement of the genitalia by the unnaturally swollen excretory vessels. In some proglottides the testes attain a maximum diameter of about 70 μ, but are generally smaller averaging about 55 μ in diameter. The cirrus-sac measures 400–600 μ in length, but may be longer as, in many instances, there are pronounced twists which tend to foreshorten it. The diameter of the cirrus-sac remains fairly constant at 40–55 μ and in some proglottides the cirrus can be seen protruding as a short nipple-like projection from the genital atrium (Text-fig. 2).

---

*Host name and number according to collection records.

The deeply-lobed ovaries are 380–520 μ by 200–240 μ and are fan-shaped. The vitelline glands, which measure 150–170 μ by 110–125 μ, tend to be surrounded by the ovarian lobes (Text-fig. 3).

The uterus breaks down into uterine capsules, each of which contains a single egg. Although initially the two uteri are quite separate, the capsules eventually fill the whole proglottis. The outer membrane of the egg measures 50–60 μ by 38-48 μ and the inner membrane measures 28–34 μ in diameter. The hooks of the oncospheres were not seen sufficiently clearly to be measured.



Figs. 1–3. *Paronia bocki* Schmelz, 1941. Early proglottis showing distribution of testes (Fig. 1), opening of cirrus-sac (Fig. 2), and part of a later proglottis showing one of the two ovaries and the associated vitelline gland (Fig. 3).

The excretory vessels appear to be unnaturally swollen and have the effect of crowding the genitalia into isolated regions in most proglottides. The transverse excretory vessel, which joins the two ventral excretory vessels posteriorly in each proglottis, is particularly prominent and swollen in fully-mature and gravid proglottides.

Discussion. Schmelz (1941) differentiates his species from *Paronia carrinoi* Diamare, 1900, on the formation of the uterus in gravid proglottides. In *P. bocki*, the two uteri eventually join to form a continuous field of uterine capsules, whereas in *P. carrinoi* both uteri remain separate. This feature, together with the difference in the size of the cirrus-sac, also serves to differentiate *P. bocki* from *P. pycnonoti*

Yamaguti, 1935. Although the number of testes in the present material may be fewer than the number described by Schmelz, and although there is a slight discrepancy in the sizes of the ovaries (380–520 μ by 200–240 μ in the present material and 700 by 290 μ in Schmelz's material) in view of the close agreement of other characters, there seems little doubt that the present material should be ascribed to *P. bocki* Schmelz, 1941. Further differences between the known species of *Paronia* can be seen readily in Table I.

P. carrinoi is listed by Yamaguti (1959) as *P. carrinii* and is included as a synonym of *P. trichoglossi* (Linstow, 1888). As indicated by Spasski (1951), Linstow, in his original description, mentions that the material is fragmented, without a scolex, and gives only the length and breadth of the fragments, the sizes of some proglottides, and the size of the eggs and oncospheres. Furthermore, Linstow indicates that " The specimens possibly belong to *Taenia leptosoma*, Diesing, found in various parrots ", and this worm, *T. leptosoma*, is now considered as belonging to the genus *Raillietina*. It would appear then that the grounds for including Diamare's species as a synonym of such an inadequately-described worm, are not really sufficient, and it is here proposed that the specific name *carrinoi* be retained and that it should not become a synonym of *P.* (?) *trichoglossi*.

Family **DAVAINEIDAE** Fuhrmann, 1907

Genus ***RAILLIETINA*** Fuhrmann, 1920

Raillietina* (*Raillietina*) *echinobothrida (Megnin, 1881)

(Text-figs. 4–8)

Taenia bothrioplites Piana, 1882.
Davainea paraechinobothrida Magalhães, 1898.
Davainea volzi Fuhrmann, 1905.
Davainea penetrans Baczynska, 1914.
Raillietina grobbeni Böhm, 1925.
Raillietina pseudoechinobothrida Meggitt, 1926

HOST. Domestic fowl (*Gallus gallus* (L.) *dom.*) 8696.

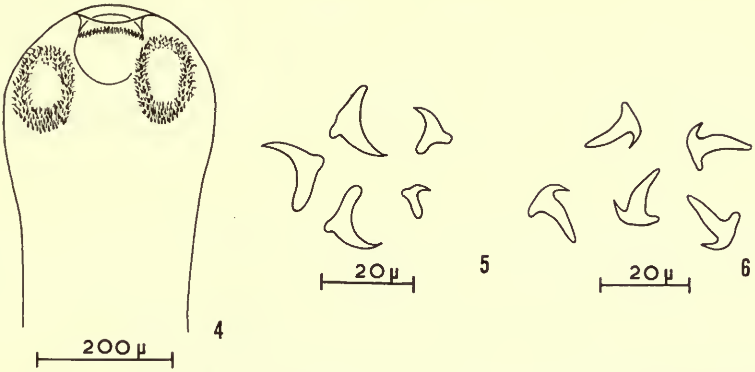
The longest specimen is 105 mm. long with a maximum breadth of about 3 mm. The proglottides are all much broader than long, the ratio of breadth to length tending to increase from immature to mature proglottides and tending to decrease from mature to gravid proglottides. The genital apertures are unilateral and are situated laterally and slightly posteriorly to the middle of each proglottis. The genital ducts pass between the dorsal and ventral excretory vessels.

The size of the scolex (Text-fig. 4) shows considerable variation, measuring 170–265 μ long by 240–330 μ broad. The four suckers are circular to oval in outline and measure 90–155 μ by 52–90 μ. They are profusely armed with spines (Text-fig. 5) which are 9–17 μ long. The rostellum, when everted, is roughly spherical with a diameter of about 100 μ. It is armed with a double circlet of about 200 hooks (Text-fig. 6) which are 12–14 μ long.

TABLE I

Paronia species to show various differences and similarities to the present material from Borneo.

Species	*Strobila*		*Scolex*	*Cirrus Sac*	*Testes*		*Gravid Uterus*	*Egg*	*Host*	*Locality*
	length in mm.	max. breadth in mm.	diameter in microns	length in microns	No.	Diameter in microns		diameter in microns		
P. ambigua (Fuhrmann, 1902)	60–80	1·5	—	120	100	60	single	30	*Amazona amazonica* RHAMPHASTIFORMES	Brazil
P. beauforti (Janicki, 1906)	18	3	—	600	360	—	single	—	*Cyclopsittacus diophthalmus* PSITTACIFORMES	New Guinea
P. biuterina Burt, 1939*a*	55	2·25	265	215–272	65–75	38	double	27–30	*Coryllinus beryllinus* PSITTACIFORMES	Ceylon
P. bocki Schmelz, 1941	70–75	5	800	700	200–220	77	single	40	*Megalaema vireus; Cyanops ramsayi* PICIFORMES	Siam
P. calcaruterina Burt, 1939*a*	126	2·1	690	380–420	102–120	85	double	31–32·5	*Molpastes haemorrhous* PASSERIFORMES	Ceylon
P. carrinoi Diamare, 1900	70–120	3–5	530	450–700	140–150	45 × 10	double	30	*Trichoglossus novaehollandiae; T. nigrigularis; Cyclopsittacus suavissimus; Lorius erythrothorax* PSITTACIFORMES	Australia; New Guinea
P. columbae (Fuhrmann, 1902)	—	1	—	90	200	—	single	30	*Columba* sp. (?); *Ptilonopus* sp. (?) COLUMBIFORMES	Sumatra; Bengal
P. coryllidis Burt, 1939*a*	70–75	1·2	305–315	325	70–80	68	single	21–24	*Coryllis beryllinus* PSITTACIFORMES	Ceylon
P. pycnonoti Yamaguti, 1935	40–55	2·5–3·2	480–580	250–400	80–125	—	double	42–48	*Pycnonotus sinensis* PASSERIFORMES	Formosa
Taenia trichoglossi von Linstow, 1888	over 80	2·1	missing	—	—	—	—	36 (outer) 26 (inner)	*Trichoglossus swainsoni* PSITTACIFORMES	Australia
P. variabilis (Fuhrmann, 1904)	70	2·5	450	270	100	40	single	43	*Rhamphastos culminatus; R. dicolorus; R. toco; R. erythrorhynchus.* PSITTACIFORMES	South America
P. zavattarii Fuhrmann and Baer, 1944	—	1·4–3·3	—	300	—	—	double	36–40	*Colius striatus* COLIIFORMES	Ethiopia
Borneo material	over 80	2	—	400–600	over 150	55–70	single	50–60 × 38–48	*Megalaema chrysopogon* PASSERIFORMES	Borneo

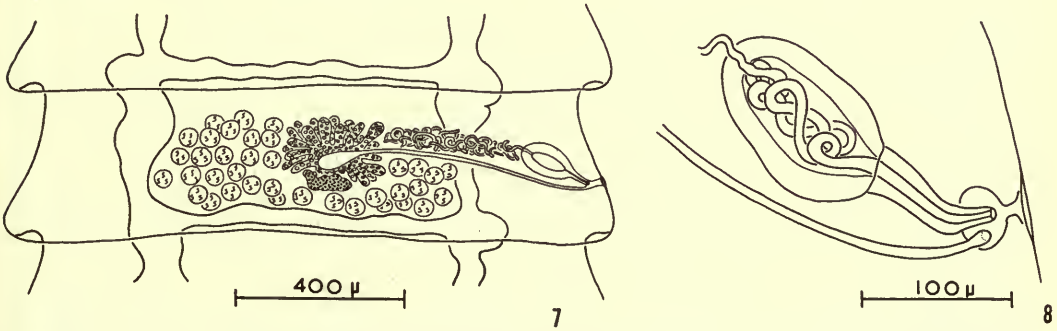


FIGS. 4–6. *Raillietina* (*Raillietina*) *echinobothrida* (Megnin, 1881). Scolex (Fig. 4), sucker spines (Fig. 5), and rostellar hooks (Fig. 6).

There are 20–45 testes which lie in two lateral fields (Text-fig. 7): those aporally comprise over half the total number. In many proglottides there are one, two or three testes which lie posteriorly or dorsally to the vitelline gland and which connect the two lateral fields.

The cirrus-sac (Text-fig. 8) measures 120–145 µ by 74–83 µ and opens into the genital atrium in the posterior half of each proglottis. It is bulbous and strongly muscled. The vas deferens is much coiled and lies in the anterior portion of each proglottis, in front of the ovary, and in fully-mature proglottides it becomes greatly distended with sperm.

The ovary which is fan-shaped and digitate lies in the middle of each proglottis. Its total breadth varies from 380 µ to 405 µ. The vitelline gland, lying immediately behind the ovary, is compact and irregularly ovoid, measuring 120–140 µ by 70–80 µ. Between the ovary and the vitelline gland lies the shell-gland which is dorsal to the receptaculum seminis. In only one proglottis could the receptaculum seminis be measured accurately, and there it measured 49 µ long by 38 µ in diameter. The vagina, in fully mature and early gravid proglottides, appears swollen with sperm in the region of the ovary.



FIGS. 7 and 8. *Raillietina* (*Raillietina*) *echinobothrida* (Megnin, 1881). Mature proglottis (Fig. 7) and cirrus-sac (Fig. 8).

The uterus is more or less sac-shaped initially, but later extends laterally beyond the excretory vessels and breaks down to form uterine capsules, which measure 110–170 μ in diameter. In over 85 % of the capsules there are four or five eggs, but occasionally two, three or six eggs may be present in a capsule. The eggs are slightly ovoid and measure 42–52 μ by 32–42 μ. The hooks of the oncosphere are 6–7 μ long.

DISCUSSION. Although the group *echinobothrida* (Megnin, 1881) (*sensu lato*) shows considerable variation among its component species or subspecies, particularly with reference to the arrangement of genital apertures, number of testes and number of eggs per capsule (see Table II), these differences do not appear to be either sufficiently great nor, and perhaps of more importance, sufficiently constant to justify the separation of any distinct species other than *echinobothrida*.

Ransom (1904) discusses fully the problems of synonymity of *echinobothrida* up to that time and more recently Lang (1929) regards the following as synonyms of *echinobothrida* (Megnin, 1881): *Davainea volzi* Fuhrmann, 1905; *Davainea penetrans* Baczynska, 1914; *Raillietina* (*R.*) *grobbeni* Böhm, 1925; and *Raillietina pseudoechinobothrida* Meggitt, 1926. As can be seen from Table II there is a wide range of overlap in most characters, even as to the arrangement of the genital apertures. Megnin (1881), Ransom (1904), López-Neyra (1920) and Meggitt (1926) all describe material with irregularly-alternating genital apertures. Ransom, however, further states that they are sometimes almost entirely unilateral. López-Neyra (1920), discussing the synonymity of those species closely related to *echinobothrida*, is of the opinion that there are two distinct varieties: the one with irregularly alternating genital apertures, which contains Megnin's original species; and the other with unilateral genital apertures, which is the variety *bothrioplitis* and which includes *Davainea paraechinobothrida* Magalhães, 1898, *D. volzi* Fuhrmann, 1905, and *D. penetrans* Baczynska, 1914. López-Neyra, however, figures part of a strobila of *echinobothrida* var. *bothrioplitis* in which the genital apertures exhibit alternation. Although Meggitt (1926*a*), in his description of *echinobothrida* (Megnin, 1881) and of *pseudoechinobothrida*, states that the genital apertures are irregularly alternate, he modified this in a letter written to D. R. R. Burt and dated 27th August, 1936, when he said: " I have looked over my slides of *R. echinobothrida* and *R. pseudoechinobothrida*, and I find that the genital aperture is invariably unilateral. I think that the mis-understanding arises from the fact that an occasional genital pore is on the wrong side, but this is so seldom as not to count." It would thus appear that the variation in the arrangement of the genital apertures is of little real significance in this species, and that what was true of Meggitt's material was probably true of the other three instances. Accordingly, as the apertures, which appear on the " wrong " side, seem to be so few these probably constitute nothing more than exceptions to the general pattern of unilateral arrangement.

While discussing the problem of synonymity of *echinobothrida* with Professor J. G. Baer, he made the interesting observation that those species within the group *echinobothrida* (*sensu lato*) show a tendency to fall naturally into two separate, smaller groups: those from Europe; and those from Asia. In the case of those species recorded from Europe there appear to be fewer testes and more eggs per capsule than in those species recorded from Asia. There is, nevertheless, some degree of overlap between these two conditions, and it probably would be unwise to do more at the present time than record this observation of differences, due apparently to geographical distribution.

It is clear that the whole question of synonymity of *echinobothrida* (*sensu lato*) will have to be gone into more fully and with more material from Asia particularly. Work is at present in hand on a large collection of cestodes from Ceylon, made by D. R. R. Burt, and it is hoped that the result of this investigation will throw more light on the above problems.

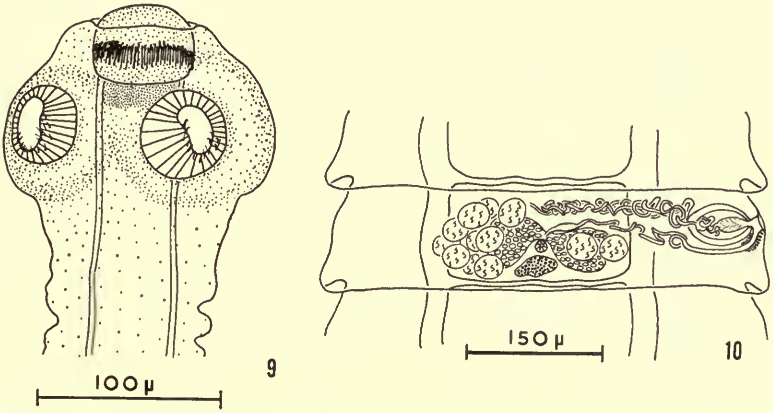
Raillietina* (*Raillietina*) *johri Ortlepp, 1938

(Text-figs. 9–10)

Raillietina (*Raillietina*) *polychalix* of Johri, 1934, *nec* Kótlan, 1921.

HOST. *Treron vernans* 8963; 9044; 9433; 9545.

The mature worms measure 50–70 mm. long by 0·6–1·0 mm. in maximum breadth. The proglottides are all broader than long, the breadth varying from two to five times the length depending upon the degree of contraction of the strobila. The genital apertures are unilateral and open in the anterior half of the margin of each proglottis. The genital ducts pass between the longitudinal excretory vessels.



FIGS. 9 and 10. *Raillietina* (*R.*) *johri* Ortlepp, 1938. Scolex (Fig. 9) and mature proglottis (Fig. 10).

The scolex (Text-fig. 9) measures 90–130 μ by 60–150 μ and bears four armed suckers. The diameter of the suckers is 40–85 μ and the spines, which are up to 10 μ long, are easily lost and were not seen in all specimens. The rostellum, 60–68 μ in diameter, bears a double crown of hooks, those in the anterior row measuring 15 μ long and those in the posterior row measuring 12 μ long.

There are 6–12 testes usually divided into two groups which lie on either side of the female genitalia (Text-fig. 10). The poral group contains one to three testes while the majority lie aporally. The testes are ovoid to spherical and measure 50–70 μ by

TABLE II

Species presently included in *Raillietina* (*Raillietina*) *echinobothrida* (*sensu lato*) to show the wide range in morphological characters.

Species:	*echinobothrida*	*botrioplitis*	*paraechinobothrida*	*echinobothrida*	*volzi*	*penetrans*	*penetrans*
Described by:	Megnin 1881	Piana 1881	Magalhães 1898	Ransom 1904	Fuhrmann 1905	Baczynska 1914	Skrjabin 1914
Strobila (length × max. breadth in mm.)	50–100×4	200×3		250×4	40–60×2	30–40×1–5	180×3
Scolex (diameter in μ)	—	350		250–450	450	352	374
Rostellum (diameter in μ)	—	140 (from drawing)		100–150	88	104	—
Rostellar hooks (number)	100	200	Differs from *echinobothrida* of Megnin only in the fact that it has unilateral genital apertures.	200	240	240	240–300
Rostellar hooks (length in μ)	8	10–15 (from drawing)		10–13	10	13	13
Suckers (diameter in μ)	large	120–130 (from drawing)		90–200	180	169	—
Sucker spines (number of rows)	7	7–8		8–10	Ant.=12–14 Post.=4–6	14–15	—
Sucker spines (length in μ)	—	6–19 (from drawing)		6–15	6–12	—	—
Testes (number)	—	—		20–30	30	15–20	30–35
Testes (diameter in μ)	—	—		—	30–36	41·6	—
Cirrus sac (length in μ)	—	—		130–180	200–230	163	163
Eggs (number per capsule)	6–7	—		6–12	8–12	—	—
Eggs (diameter in μ)	90	—		25–50	20–25	—	—
Oncospheres (diameter in μ)	—	—		—	13	10·4	—
Genital apertures (arrangement)	Irregularly alternating	Unilateral		Irregularly alternating	Unilateral	Unilateral	Unilateral

Species:	*echino-bothrida*	*echinobothrida* var. *bothrio-plitis*	*grobbeni*	*pseudo-echino-bothrida*	*echino-bothrida*	*echino-bothrida*	*echino-bothrida*	*Borneo material*
Described by:	López-Neyra 1920	López-Neyra 1920	Böhm 1925	Meggitt 1926*a*	Lang 1929	Sawada 1955	Yamaguti 1956	
Strobila (length × max. breadth in mm.)	150 × 4	230 × 4	170–440 × 4·1	80–90 × 1·8	35–200 × 3	120–250 × 4	60–160 × 2·4	105 × 3
Scolex (diameter in μ)	250–450	250–450	344	—	286–343	250–550	250–400	170–265
Rostellum (diameter in μ)	88–150	88–150	96	—	96–107	100–140	100–130	100
Rostellar hooks (number)	200–240	200–240	200	200	120–140	200	—	200
Rostellar hooks (length) in μ	10 & 13	10 & 13	10 & 13	8–12	10 & 13	10–13	10 & 12	12–14
Suckers (diameter in μ)	90–200	90–200	125	—	120–140	130–200	210	52–115
Sucker spines (number of rows)	10–15	10–15	—	—	8–12	10–13	9–14	Several
Sucker spines (length in μ)	6–15	6–15	7–17	—	5–15	4–20	up to 12	9–17
Testes (number)	20–?	20–35	24–32	30–50	25–45	25–45	38–48	20–45
Testes (diameter in μ)	39–43	39–43	54	—	38–67	—	24–60	35–60
Cirrus sac (length in μ)	130–200	130–190	182–187	—	150–200	150–165	120–190	120–145
Eggs (number per capsule)	8–12	8–12	up to 6	3–4	4–10	3–8	5–9	2–6
Eggs (diameter in μ)	25–40	25–40	24–37	—	34–48	73–77	27–42	32–52
Oncospheres (diameter in μ)	10–14	10–14	10–15	—	10–18	24–26	10–15	12–18
Genital apertures (arrangement)	Irregularly alternating	Unilateral	Unilateral	Irregularly alternating	Unilateral	Unilateral or Irregularly alternating	—	Unilateral

36–60 μ. The cirrus-sac, 85–115 μ long by 40–60 μ in diameter, is roughly flask-shaped and has a thick muscular wall. In a few proglottides the profusely armed cirrus could be seen as a small bulbous projection from the genital atrium. There is an internal seminal vesicle with a diameter of 15–30 μ. The vas deferens is much coiled and lies parallel to the anterior margin of each proglottis.

The bilobed ovary lies in the centre of the proglottis and measures 115–135 μ across both lobes. The vitelline gland, situated posteriorly to the isthmus of the ovary, is compact and measures 45–75 μ by 30–55 μ. The shell-gland, 20–25 μ in diameter, lies more or less centrally over the isthmus of the ovary, occasionally being slightly displaced so that it lies partly over one of the lobes of the ovary. The vagina expands before reaching the centre of the proglottis to form a receptaculum seminis, 25–45 μ long by 15–25 μ in diameter. The opening of the vagina is posterior to the opening of the cirrus-sac.

The uterus breaks down to form 18–30 capsules per proglottis and occasionally more, the size of the capsules varying from 50–80 μ in long diameter by 40–65 μ in short diameter. In some few capsules, which contained more than the normal number of eggs, the long diameter reached as much as 100 μ or more. There are 8–12 eggs per capsule usually, while some capsules contained as few as 6 and others as many as 16 eggs. The eggs measure 35–40 μ by 27–33 μ and the contained oncospheres are about 15 μ in diameter.

Discussion. *Raillietina* (*Raillietina*) *polychalix* Kótlan, 1921, was described by Johri (1934) from *Psittacula krameri manillensis* and from *Columba livia domestica*, although the worms from *Columba* differed quite markedly from those found in *Psittacula*. According to Johri, however, these differences are not sufficiently great to warrant separation of the worms and the erection of a new species, and accordingly the worms from both hosts were identified as *polychalix*. Ortlepp (1938), however, feels that the differences between the worms from *Columba* and those from *Psittacula* are too great to allow the inclusion of both groups of worms in the species *polychalix* and erects a new species, *Raillietina* (*Raillietina*) *johri*, to contain those worms which were found in *Columba livia domestica*. The two differences that Ortlepp considers to be most significant are the different sizes of the cirrus-sac and the different number of rostellar hooks (See Table III).

Table III

Raillietina (*Raillietina*) *polychalix* Kótlan, 1921, as described by Johri (1934).

Host	Number of rostellar hooks	Length of cirrus sac
Columba	324	125–130μ
Psittacula	190	61μ

Perhaps it should also be pointed out that the worms described by Johri that came from *Psittacula* show even less similarity to Kótlan's species *polychalix* than did the worms from *Columba*, and accordingly it would appear that neither of the worms which Johri described is in fact *polychalix* Kótlan. Proper identification of the worms from *Psittacula* will have to await a full re-examination of the material and comparison with known species.

The present material agrees well with the few characters that are given for *Raillietina* (*Raillietina*) *johri* and also seems to differ in one or more characters from all other species of *Raillietina* from birds, where the size of rostellar hooks is within the same range of 12–15 μ, and where the number of testes also falls within the same range of 6–12 testes per proglottis (See Table IV). As can be seen, the only species with which the present material does not differ significantly, apart from *johri*, is *Raillietina* (*R.*) *circumcincta* (Krabbe, 1869) but this worm is very poorly described and furthermore comes from a well-separated order of birds, the Ciconiiformes.

According to the label in one of the tubes containing worms of the present species the host is *Tringa glareola*, a charadriiform bird, but as there does not appear to be any substantiated record of a *Raillietina* from any member of the Charadriiformes (see discussion following description of *Kowalewskiella susanae* n. sp.), it is not unlikely that there may have been a mix-up in the labels. All measurements of the present material from *Tringa glareola* are recorded separately, as follows, to facilitate comparison in the event of there being any further recorded *Raillietina* from a Charadriiform bird.

Strobila—41 × 1·15 mm.; scolex—165 × 210 μ; rostellum—100 μ diam.; rostellar hooks—200–250 hooks, in double circle, about 12 μ long (size measured from whole mount); suckers—armed, 65–70 μ in diameter; genital apertures—unilateral; testes—6–11, 37–52 μ in diameter, on both sides of the female genitalia; cirrus-sac—95–130 μ by 50-75 μ; internal seminal vesicle present; ovary–bilobed; vitelline gland—median, posterior to ovary, ovoid; receptaculum seminis—59 μ × 45 μ; egg capsules—not extending beyond longitudinal excretory vessels, containing about seven eggs per capsule.

Raillietina* (*Raillietina*) *parviuncinata Meggitt et Saw, 1924

(Text-figs. 11–13)

HOST. Domestic fowl (*Gallus gallus* (L.) *dom.*) 8696.

The mature worm measures 35 mm. long by 0·9 mm. in maximum breadth. The proglottides are broader than long, but only immature and early mature ones are present. The genital apertures are unilateral and open in the anterior half of the margin of each proglottis.

The scolex (Text-fig. 11) measures 170 μ long by 240 μ in diameter and bears four, heavily armed suckers. The suckers are oval measuring 92–100 × 52–66 μ and the sucker spines, while being difficult to measure accurately, appear to reach up to 12 μ long. The rostellum is not evaginated and bears a complete double row of about 200 hooks which are 8–10 μ long.

In the early mature proglottides present, the testes number 20 to 30 and are 38–46 × 34–43 μ. The cirrus-sac was not clearly seen, but appears to be about 70–80 μ long by about 40–50 μ in diameter.

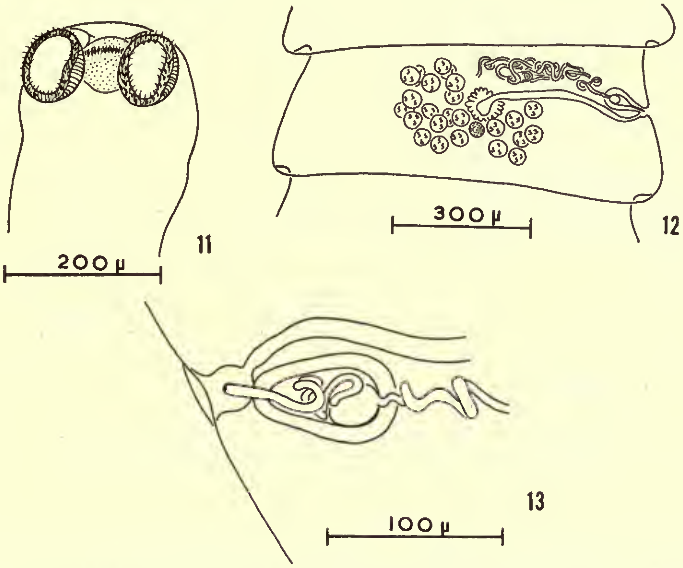
DISCUSSION. Although there are several discrepancies between the present material and those worms described by Meggitt and Po Saw (1924), it is apparent

TABLE IV

Raillietina (*Raillietina*) species from birds with rostellar hooks in the range 12–15μ long and with 6–12 testes.

Species:	*circumcincta*	*micracantha*	*micracantha*	*provincialis*	*spiralis*	*bycanistis*	*polychalix*	*polychalix*	*johri*	
	Krabbe, 1869	Fuhrmann, 1909	Fuhrmann, 1909	Linstow, 1909	Baczynska, 1914	Baylis, 1919	Kótlan, 1921	Kótlan, 1921	Ortlepp, 1938	Borneo material
Description taken from:	Krabbe 1869	Fuhrmann 1909	López-Neyra 1931	Linstow 1909	Baczynska 1914	Baylis 1919	Kótlan 1921	Johri 1934	Ortlepp 1938	
Strobila (length × max. breadth in mm.)	120 × 2	100 × 0·8	180 × 1·2	60 × 1·58	30–40 × 1·28	140 × 2	55 × 1·7	103	273 × 0·75	50–70 × 1
Scolex (diameter in μ)	—	180	180–200	280	224	270	320	—	260	90–130
Rostellum (diameter in μ)	—	—	117–135	—	150	150	148	—	—	60–68
Rostellar hooks (number)	300	200	150	500	300	—	240–250	190	324	
Rostellar hooks (length in μ)	11–12	13–14	12–14·7	14·3	15·6	15	13	13·5 & 19	11 & 14	12 & 15
Suckers (diameter in μ)	—	—	50–65 × 40–50	130	52	88	—	—	—	40–85
Sucker spines (length in μ)	—	—	9–10	—	—	13	—	—	6–7	10
Testes (number)	—	—	14–18	10–12	6–7 (by implication)	12–14	10–12	9–11	8–9	6–12
Testes (diameter in μ)	—	—	50 × 45	57–68	39	75	40	—	—	50–70 × 36–60
Cirrus sac (length × diameter in μ)	—	—	110–140 × 40–60	—	101	200 × 62	120	61	125–130	85–115 × 40–60
Eggs (number per capsule)	—	—	4–7	several	4–6	4–5	2–5	—	6	8–12 (6–16)
Eggs (diameter in μ)	—	—	38–42 × 35–40	52	—	—	—	—	—	35–40 × 27–33
Oncospheres (diameter in μ)	—	—	14–15	18	—	15	—	—	—	15
Avian host (order)	Ciconii-formes	Columbi-formes	Columbi-formes	Galli-formes	Columbi-formes	Coracii-formes	Psittaci-formes	Psittaci-formes	Columbi-formes	Columbi-formes

that in their description there are several typographical errors. The maximum breadth of the worm, for instance, is quoted as being 0·2 mm. and yet in the text-figure on page 325 a mature proglottis is drawn which, according to the scale given, measures over 1·0 mm. in breadth. The cirrus-sac in their description is described as being 0·58 to 0·84 mm. in length, whereas it is again clear from the drawing on page 325 that the length should be 0·058 to 0·084 mm.



Figs. 11–13. *Raillietina* (*R.*) *parviuncinata* Meggitt et Saw, 1924. Scolex (Fig. 11), mature proglottis (Fig. 12), and cirrus-sac (Fig. 13).

In view of the close agreement between the length of rostellar hooks (7–9 μ—Meggitt and Po Saw; 8–10 μ—present material); the number of testes (24–39—Meggitt and Po Saw; 20–30—present material); and the length of the cirrus-sac (58–84 μ—Meggitt and Po Saw; 70–80 μ—present material) the present material is tentatively identified as *Raillietina parviuncinata*. This identification should remain tentative owing to the fact that *parviuncinata* was recorded initially from an anseriform bird, whereas the present material comes from a galliform bird. So far as can be ascertained, however, the present worms do not resemble any known species from a galliform bird well enough to warrant identification with them.

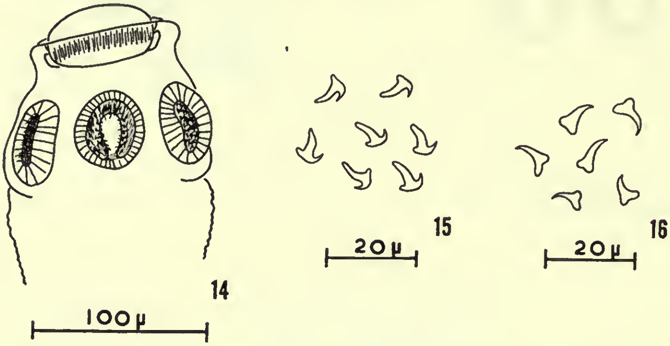
Raillietina* (*Raillietina*) *sequens Tubangui et Masiluñgan, 1937

(Text-figs. 14–18)

Hosts. Domestic pigeon (*Columba livia* domestica L.) 9019. *Streptopelia chinensis* 9409, 9151. *Aegithina tiphia* 9047.

The largest worm measures 100 mm. in length and the maximum breadth is 1·5 mm. The proglottides are all broader than long, with the ratio of breadth to length generally increasing towards the posterior end of the worm. The genital apertures are unilateral and the genital ducts pass between the excretory vessels.

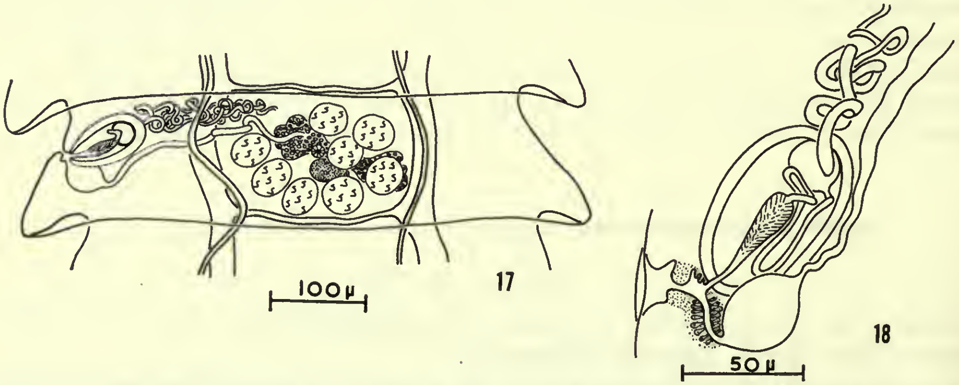
The scolex (Text-fig. 14) varies in diameter from 80 to 122 μ and bears a rostellum which measures 45–90 μ (everted and withdrawn) in diameter by 30–53 μ long. The rostellar hooks (Text-fig. 15) are arranged in two separate rows; those of the anterior row being slightly larger, measuring 7·5–8 μ in length while those of the posterior row measure only 6–7 μ in length. The four suckers measure 30–51 μ × 20–45 μ and are armed with spines (Text-fig. 16) which are 2–10 μ long.



Figs. 14–16. *Raillietina* (*R.*) *sequens* Tubangui et Masiluñgan, 1937. Scolex (Fig. 14), rostellar hooks (Fig. 15), and sucker spines (Fig. 16).

There are 6–10 testes (Text-fig. 17) one to three usually lying porally, which measure 45–60 μ × 40–55 μ. The cirrus-sac (Text-fig. 18) is 80–115 μ long × 40–60 μ in diameter and contains a slightly coiled cirrus, which is armed with hair-like, cuticular spines, and an internal seminal vesicle of 35–40 μ by about 30 μ. The vas deferens becomes greatly swollen with sperm and highly twisted.

The ovary is bilobed with each of the two lobes tending to subdivide further into smaller lobules. It is situated medially and ventrally being contained within the confines of the ventral excretory vessels. The vitelline gland, lying immediately



Figs. 17 and 18. *Raillietina* (*R.*) *sequens* Tubangui et Masiluñgan, 1937. Mature proglottis (dorsal view) (Fig. 17) and cirrus-sac (ventral view) (Fig. 18).

posteriorly to the ovary, is irregularly ovoid and measures 30–40 μ in diameter. Immediately in front of the vitelline gland, but posterior to the ovary, is the shell-gland of 20–25 μ in diameter. The receptaculum seminis is just posterior to the cirrus-sac and tends, in many cases, to lie slightly ventrally to it. It is highly variable in size, measuring up to 50 μ × 25 μ.

The uterus, which arises immediately dorsally to the shell-gland, is initially a sac-like structure, but eventually occupies the whole of the medulla before breaking down into uterine capsules. The number of capsules per proglottis is variable, but generally falls between 50–70, each capsule measuring 50–100 μ × 35–55 μ. There are 2–8 oncospheres per capsule and these measure 25–40 μ × 15–35 μ. The hooks of the oncospheres are small, ranging from 5·5 μ to about 7 μ in length.

DISCUSSION. As can be seen in Table V there are several worms which have only a few testes and which also possess small rostellar hooks. In many instances the only difference between separate species is that one species may have one or two testes more, or fewer, than another. This hardly seems to be a justifiable criterion for the erection of new species, as it is abundantly clear in the present material that the range in number of testes is fairly wide. However, it should be noted that this range of 6–10 testes has not been seen in any single worm, but represents the total range in all the worms which otherwise are more or less identical from the different hosts mentioned. Thus, some individual worms show a range of 6–7 testes; others a range of 6–8; others a range of 8–10 and so on. While this observation could be interpreted as indicating that there are two or more separate species present, in view of the extremely close similarity of other features, and the fact that there is no other constant difference manifest between worms showing differences in number of testes, it is here proposed that the range of 6–10 testes represents an intraspecific variation in the species *R. sequens*. Furthermore a re-examination of the species listed in Table V, and also many other species in the genus *Raillietina*, may very well show that the intraspecific variation is so great that several species which at present are considered as distinct should in fact be united into a single species. In view of the fact that it has not been possible, as yet, to see sufficient type-material, redescriptions from the suggested re-examination will not be presented at this time.

Except in the number of testes, as has just been discussed, the present material appears to agree in all respects with worms described by Tubangui and Masiluñgan (1937) as *Raillietina* (*R.*) *sequens* and is, accordingly, here identified as that species.

***Raillietina* (*Raillietina*) *allomyodes* Kótlan, 1921**

(Text-fig. 19)

HOST. *Treron vernans* 8951.

One mature, but non-gravid, worm was present. It measures 15 mm. long and has a maximum breadth of 0·8 mm. The worm is highly contracted and accordingly the shape of the proglottides, which ranges from 24 times broader than long in immature proglottides to 11 times broader than long in the last mature proglottides, is of little significance. The genital apertures are unilateral.

TABLE V

Raillietina species possessing rostellar hooks under 10 μ long and with 5–10 testes.

Species:	*cryptacantha* Fuhr., 1909	*paucitesticulata* Fuhr., 1909	*cacatuina* Johnst., 1911–13	*calyptomenae* Baylis, 1926	*flabralis* Meggitt, 1927	*flaminiata* Meggitt, 1931	*fragilis* Meggitt, 1931	*fulvia* Meggitt, 1933	*sequens* Tub. & Mas., 1937	Borneo material
Descriptions taken from:	Fuhrmann (1909)	Fuhrmann (1909)	López-Neyra (1931)	Baylis (1926)	Meggitt (1927*a*)	Meggitt (1931)	Meggitt (1931)	Meggitt (1933)	Tubangui & Masiluñgan (1937)	
Strobila (length × max. breadth in mm.)	120×1·5	100×0·6	50×0·53	60–100×1·15	350×1	50×0·6	190×0·9	?×6·0	170×1·1	100×1·5
Scolex (diameter in μ)	140	100	114	170–250	216	720	150	110–120	100	80–122
Rostellum (diameter in μ)	59	44	—	100–125	80	—	73	35–40	60	45–90
Rostellar hooks (number)	170	120	—	Very numerous	350	—	—	—	180	—
Rostellar hooks (length in μ)	7·2	9–10	Ca. 6	8	6	9	6–9	—	7·6–8	6–8
Suckers (diameter in μ)	36	27	45	55–80	—	—	—	—	40	30–51× 20–45
Sucker spines (number of rows)	—	—	Several	—	—	—	several	several	—	several
Sucker spines (length in μ)	—	—	7·5	minute	—	—	—	—	—	2–10
Testes (number)	8–12	6–7	4–5	5	4–5	5–9	8–9	8–10	5–6	6–10
Testes (diameter in μ)	68	—	20	—	—	—	—	—	55–70	40–60
Cirrus sac (length × diameter in μ)	—	120–140	65–100× 20–42	160× 55	up to 120	110–130× 40–60	120× 60	92–106× 54–64	100–120× 40–60	80–115× 40–60
Eggs (number per capsule)	—	6–8	12	8	10	2–6	4–6	1	2–8	2–8
Eggs (diameter in μ)	—	—	45×19	—	—	—	—	—	34·5–46	—
Oncospheres (diameter in μ)	—	—	—	—	—	—	—	35–40	19–23	25–40× 15–35
Genital apertures (arrangement)	Unilateral	Unilateral	Unilateral	Unilateral	Unilateral	Unilateral	Unilateral	Unilateral	Unilateral	Unilateral
Avian host (order)	Columbiformes	Columbiformes	Psittaciformes	Passeriformes	Coraciiformes	Columbiformes	Columbiformes	Columbiformes	Columbiformes	Columbiformes

The scolex (Text-fig. 19) measures 200 μ long by 270 μ in diameter and bears a rostellum of 150 μ in diameter. The rostellar hooks, which number about 210, are present in a double circlet around the rostellum and are of two distinct sizes: those of the anterior row measuring 18 μ in length and those of the posterior row measuring 21 μ in length. The four suckers are ovoid, measuring 75–85 μ × 68–77 μ, and are armed with three or four rows of thorn-shaped spines which vary from 5 μ to 10 μ long.

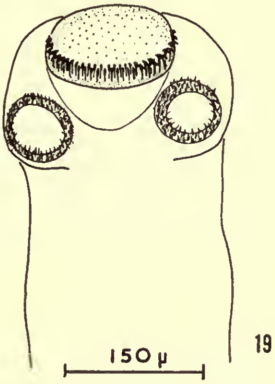


FIG. 19. *Raillietina* (*R.*) *allomyodes* Kótlan, 1921. Scolex.

There are 7–9 testes in each proglottis and in mature proglottides these are 30–50 μ in diameter. The cirrus-sac, which opens laterally in the anterior half of each proglottis, is 100–130 μ long by about 60 μ in diameter and contains a cirrus armed with long fine hairs. There is an internal seminal vesicle at the base of the cirrus-sac and this measure 20–25 μ in diameter. Leading into the seminal vesicle is a highly convoluted vas deferens which runs parallel to the anterior margin of each proglottis.

The ovary is bilobed and is situated centrally in a ventral position. The vitelline gland, which lies immediately posteriorly to the isthmus of the ovary, measures 20–35 μ × 90–105 μ. There is a distinct swelling of the vagina, adjacent to the genital aperture, which measures 35–45 μ × 20–25 μ and which probably functions as a receptaculum seminis.

DISCUSSION. Table VI lists those species of *Raillietina* which possess rostellar hooks in the range 18–21 μ, and which possess less than 20 testes. As is suggested in the discussion following the description of *Raillietina* (*R.*) *sequens*, it seems probable that several of the different species listed may well be intraspecific varieties of a single species. For instance, the only real difference between *allomyodes* and *columbiella* lies in the lengths of the cirrus-sacs which are 120–150 μ and 160–230 μ respectively. Without a thorough re-examination of the type-material, it is not possible to state that these names are synonymous, but it could well be the case that the cirrus-sacs in *allomyodes* were measured in younger proglottides or, more probably, that the smaller size may be explained in terms of a difference in host-species. Similarly, it is quite clear from Table VI that *taiwanensis* and *weissi* are similar in most respects, differing only in that the former has 14–17 testes while

TABLE VI

Raillietina species with less than 20 testes and with rostellar hooks in the range 18–21 μ

Species:	*filiformis* Vigueras, 1960	*oligocantha* Fuhrmann, 1909	*allomyodes* Kótlan, 1921	*aruensis* Fuhrmann, 1911	*columbiella* Ortlepp, 1938	*flaccida* Meggitt, 1926	*frayi* Joyeux & Houdemer, 1927	*lutzi* Parona, 1901
Description taken from:	Sawada (1964)	Fuhrmann (1909)	Kótlan (1921)	Fuhrmann (1911)	Ortlepp (1938)	Meggitt (1926*b*)	Joyeux & Houdemer (1927)	Parona (1901)
Strobila (length × max. breadth in mm.)	54×0·4	50–80×1	60×0·76	100×2	34–67×2	130–150×1·2	71×1·5	52–60×1
Scolex (diameter in μ)	—	370	289	300–38 (=380?)	188–270	—	310–350	250
Rostellum (diameter in μ)	—	110	—	110	120–180	—	140	—
Rostellar hooks (number)	90–100	34	160–200	180–200	200	150	350	—
Rostellar hooks (length in μ)	20–21	21–23	17–18	18	19–22 & 16–18	17 & 22	16–18	20
Suckers (diameter in μ)	—	180	78	90–100	58–80× 70–90	—	70–90	—
Sucker spines (length in μ)	—	—	—	—	up to 10	—	12–15	—
Testes (number)	10–12	—	12–16	20	11–13	14–17	13	—
Testes (diameter in μ)	—	—	40	50–60	63–77	—	30–45	—
Cirrus sac (length × diameter in μ)	—	160×?	120–150×?	150×?	160–230× 50–87	100×?	175×50	—
Eggs (number/capsule)	1	1	6–7	—	4–8	8–9	12	—
Eggs (diameter in μ)	—	40–48	—	—	—	—	—	—
Oncospheres (diameter in μ)	—	36	—	—	—	—	12	—
Genital apertures (arrangement)	Unilateral	Irregularly alternating	Unilateral	Unilateral	Unilateral	Unilateral	Unilateral	Unilateral
Avian host (order)	Columbiformes	Crypturiformes	Columbiformes	Psittaciformes	Columbiformes	Columbiformes	Columbiformes	Piciformes

Species:	*lutzi* Parona, 1901	*nagpurensis* Moghe, 1925	*penetrans nova* Johri, 1934	*permista* Southwell & Lake, 1939	*polychalix* Johri, 1934 (in part.) *nec* Kótlan, 1921	*taiwanensis* Yamaguti, 1935	*weissi* Joyeux, 1923	*weissi* var. *valliclusa* Joyeux & Baer, 1936	Borneo material
Description taken from:	Fuhrmann (1909)	López-Neyra (1931)	Johri (1934)	Southwell & Lake (1939)	Johri (1934)	Yamaguti (1935)	Joyeux (1923)	Sawada (1965)	
Strobila (length × max. breadth in mm.)	60 × 1	250–274 × 1·9	248 × 0·67	30 × 1·5	—	170 × 1·8	142 × 2	140–150 × 2	15 × 0·8
Scolex (diameter in μ)	470	339–382	250	240	103	240–280	150–170 (& up to 260)	150–170	270
Rostellum (diameter in μ)	70	216–241	—	—	—	150–180	100	100–150	150
Rostellar hooks (number)	100	220	154–184	36	190	200	150–300	200–250	210
Rostellar hooks (length in μ)	18–19	17–19	14 & 19	18	13·5–19	19	16 & 19	20–25	18 & 21
Suckers (diameter in μ)	110	142 × 114	—	136	—	60–84	44–60	40–60	75–85 × 68–77
Sucker spines (length in μ)	—	7	—	—	—	8–10	10	10	5–10
Testes (number)	—	19–22	16–19	15–20	9–11	14–17	12	12–15	7–9
Testes (diameter in μ)	—	72–78	—	—	—	—	60–80	—	30–50
Cirrus sac (length × diameter in μ)	—	90–111 × 30–42	125–134 × ?	ca. 105 (from drawing)	6 × ?	100–120 × 28–42	100–130 × 25–40	100–130 × 25–40	100–130 × 60
Eggs (number/capsule)	12–16	3–8	5–7	6	—	3–8	6	6	—
Eggs (diameter in μ)	—	50 × 43	—	—	—	36–42	33–43	43	—
Oncospheres (diameter in μ)	—	17 × 14	47–55	—	—	—	18	18	—
Genital apertures (arrangement)	Unilateral	Unilateral	Unilateral	Unilateral	Unilateral	Unilateral	Unilateral	Unilateral	Unilateral
Avian host (order)	Piciformes	Columbiformes	Passeriformes	Piciformes	Psittaciformes	Columbiformes	Columbiformes	Columbiformes	Columbiformes

the latter possesses only 12 testes. Looking at the variety *weissi valliclusa*, however, it is clear that the range quoted for this variety, of 12–15 testes, falls exactly between the ranges for the two species just mentioned. Furthermore, in view of the evidence presented in the discussion on *Raillietina* (*R.*) *sequens* it would appear that the number of testes can show a relatively wide range within a single species and accordingly not only would *taiwanensis* and *weissi* be synonymous, but, further, these would simply represent variations of Kótlan's species, *allomyodes*. Although it is not intended that these, or any others, be united into a single species at the present time, the possibility that a difference in host-species may affect differently the morphological development of the infesting worms is obviously a strong possibility which warrants experimental verification.

The present material differs in at least one respect from all the other species described, but in view of the close similarity of *allomyodes*, *taiwanensis* and *weissi* to each other and to the present worms, these are identified as belonging to that group all members of which should, on grounds of priority, be referred to the species *allomyodes*.

Raillietina (***Raillietina***) sp.

Host. *Treron curvirostra* 9265.

The strobila measures 50 mm. long by 1·15 mm. in maximum breadth. Nearly all the segments are much broader than long although the last few segments have a tendency to become square or slightly longer than broad. The genital apertures are unilateral and situated in the anterior half of each proglottis.

The scolex is missing.

There are 20–24 testes which measure 45–60 μ × 23–37 μ and which are situated in two groups on either side of the female genitalia. The group on the aporal side contains more than that on the poral side. The cirrus-sac is long and unusually thin, measuring 110–125 μ long by only 15–25 μ in diameter. No seminal vesicle was seen and in none of the proglottides was the cirrus extruded. The vas deferens lies in large loose coils in the anterior, poral moiety of each proglottis.

The ovary is bilobed, each of the two lobes being digitate, and is situated centrally in the proglottis. The vitelline gland, 37–45 μ × 15–23 μ, is compact and irregularly lobed, lying immediately behind the ovary.

The uterus breaks down to form about 25 capsules per proglottis which measure 115–150 μ × 85–100 μ. In each capsule there are 6–9 eggs which measure 28–32 μ × 20–25 μ, while the contained oncospheres are about 14 μ in diameter.

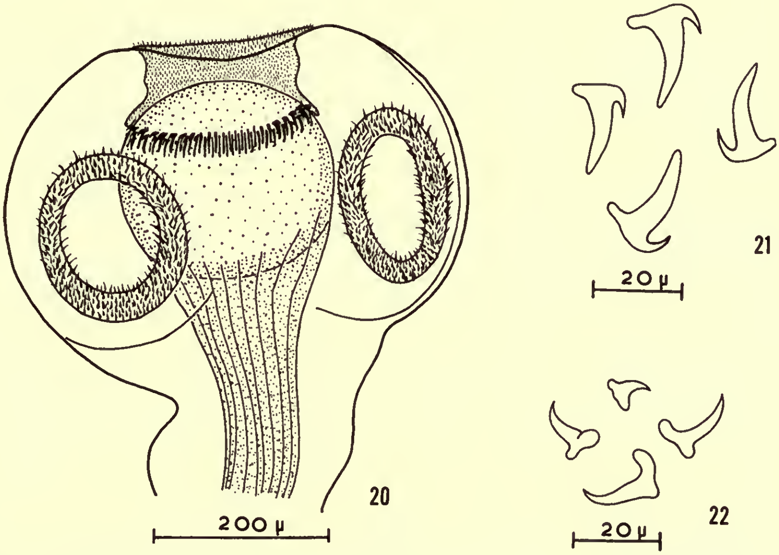
Discussion. Table VII contains those species of *Raillietina* (*Raillietina*) which: (a) parasitize birds; (b) possess a number of testes which falls in the range 20–24; and (c) possess a cirrus-sac the length of which falls in the range 100–150 μ. As can be seen from the table, the present material agrees reasonably well with several species, but does not agree in every respect with any single species. However, in view of the fact that the scolex is missing and in view of the reasonable similarity to several other species this worm has neither been given the status of a new species, nor has it been identified with any existing species.

Raillietina* (*Paroniella*) *siamensis Schmelz, 1941

(Text-figs. 20–24)

HOSTS. *Megalaema chrysopogon* 8750, 8891, 9418; *Meiglyptes tukki* 9274; *Charadrius leschenaultii* 9486.

The longest specimen is 35 mm. and the maximum breadth from any of the worms is 1·15 mm. The proglottides are all broader than long and in mature proglottides the breadth varies from two to four times the length. The genital apertures are unilateral and the genital ducts pass between the dorsal and ventral excretory canals.



FIGS. 20–22. *Raillietina* (*Paroniella*) *siamensis* Schmelz, 1941. Scolex (Fig. 20), rostellar hooks (Fig. 21), and sucker spines (Fig. 22).

The scolex (Text-fig. 20) measures 490–525 μ across the region of the suckers and has a length of about 350 μ. The rostellum is 174–215 μ in diameter by 140–178 μ in length and bears a double crown of about 200–300 hammer-shaped hooks (Text-fig. 21). The hooks in the anterior row are larger than those of the posterior row; the former being about 28 μ long while the latter are only 19–23 μ long. There are four well-developed suckers, armed with spines (Text-fig. 22) of 8–18 μ in length. In some specimens the anterior part of the scolex could be seen to be covered with hair-like spines less than 3 μ long. This was easily seen where the rostellum was invaginated.

There are 20–40 testes (Text-fig. 23) which lie in two separate fields; the larger group lying aporally comprising 12–30 testes. The testes measure 40–90 μ × 37–68 μ. The cirrus-sac has a length of 90–130 μ and a maximum diameter of 60–74 μ. It has a thick wall of about 8 μ and opens into the genital atrium anteriorly to the opening of the vagina in the anterior half of the lateral margin. There is neither

TABLE VII

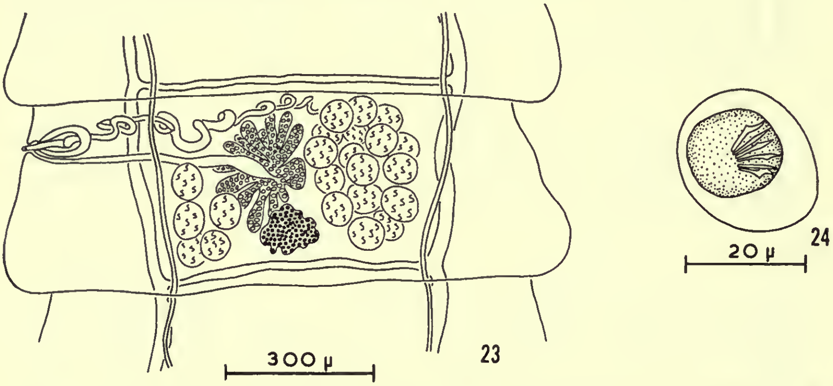
Raillietina (*Raillietina*) species with testes in the range 20–24 and with cirrus sacs in the range 100–150μ in length

Species:	*aruensis* Fuhrmann, 1911	*debilis* Baylis, 1919	*goura* Fuhrmann, 1909	*grobbeni* Böhm, 1925	*kantipura* Sharma, 1943	*korkei* Joyeux & Houdemer, 1927	*leiopoae* Johnst. & Clark, 1948
Description taken from:	Fuhrmann (1911)	Baylis (1919)	Fuhrmann (1909)	Böhm (1925)	Sharma (1943)	Joyeux & Houdemer (1937)	Sawada (1965)
Strobila (length × max. breadth in mm.)	100×2	45×3	170×1·1	170–440	160–180×0·85	164×2	3–6
Scolex (diameter in μ)	300–38 (=380)?	200	180–200	344	220	200	650
Rostellum (diameter in μ)	110	80	100	96	120	120–130	240–280
Rostellar hooks (number)	180–200	enormous number	300	100–200	180–200	150–160	133–154
Rostellar hooks (length in μ)	18	8	9	13 & 10	20–22	18–20	39–52
Suckers (diameter in μ)	90–100	—	50	125×95	55	60–70	160
Sucker spines (length in μ)	—	12	—	7–17	4	up to 10μ	6–8
Testes (number)	20	at least 30	18–20	24–32	16–26	at least 24	22–23
Testes (diameter in μ)	50–60	—	60	54	—	35	—
Cirrus sac (length × diameter in μ)	150	125×60	120–140	112–117× 79–84	110 × 48	105–110×50	100–130× 60–70
Eggs (number/capsule)	—	4–5	8–10	up to 6	3–6	6–9	21–26
Eggs (diameter in μ)	—	—	—	—	—	18×14	—
Oncospheres (diameter in μ)	—	15	—	—	—	—	11–14
Genital apertures (arrangement)	Unilateral	?	Unilateral	Unilateral	Unilateral	Unilateral	Unilateral
Avian host (order)	Psittaciformes	Ciconiiformes	Columbiformes	Galliformes	Columbiformes	Columbiformes	Galliformes

Species:	*macroscolecina* Fuhrmann, 1909	*michaelseni* Baer, 1925	*nagpurensis* Moghe, 1925	*nripendra* Sharma, 1943	*permista* Southwell & Lake, 1939	*pintneri* Klaptocz, 1906	*werneri* Klaptocz, 1908	Borneo material
Description taken from:	Fuhrmann (1909)	Baer (1925)	Moghe (1925)	Sharma (1943)	Southwell & Lake (1939)	López-Neyra (1931)	Klaptocz (1908)	
Strobila (length × max. breadth in mm.)	60–80 × 1	55–60 × 0·82	250–274 × 1·9	200–250 × 1·25	30 × 1·5	35–72 × 1·4	55	50 × 1·15
Scolex (diameter in μ)	380–430	420	339–382	187	240	219	200	Scolex missing
Rostellum (diameter in μ)	200	—	216–241	110	—	42	75	
Rostellar hooks (number)	350	200–240	220	150–180	36	200	200	
Rostellar hooks (length in μ)	—	12·8–13	19 & 17	12	18	6·4–8	—	
Suckers (diameter in μ)	—	76	142 × 114	62	136	100	30–45	
Sucker spines (length in μ)	—	8	7	—	—	7–8	7–8	
Testes (number)	20	14–17	19–22	18–24	15–20	18–20	15–25	20–24
Testes (diameter in μ)	30–40	40	78 × 72	—	—	40	70–80 × 40–45	45–60 × 23–37
Cirrus sac (length × diameter in μ)	120	87–114 × 76	90–111 × 30–42	120 × 55	Ca. 100 (from drawing)	100 × 70	100 × 46–58	110–125 × 15–25
Eggs (number/capsule)	8–10	4–6	5–6	4–9	6	15	—	6–9
Eggs (diameter in μ)	—	—	50 × 43	—	—	50	—	28–32 × 20–25
Oncospheres (diameter in μ)	—	15·2	17 × 14	—	—	19–23	—	14
Genital apertures (arrangement)	Unilateral	Unilateral	Unilateral	Unilateral	Unilateral	Unilateral	Unilateral	Unilateral
Avian host (order)	Psittaciformes	Columbiformes	Columbiformes	Columbiformes	Piciformes	Galliformes	Coliiformes	Columbiformes

an internal nor an external seminal vesicle, although in fully-mature and gravid proglottides, the vas deferens becomes greatly swollen with sperm and may act as an external seminal vesicle. In early proglottides the vas deferens tends to lie along the anterior edge of the segment, but, as it becomes filled with sperm, it comes to occupy most of the anterior poral quarter of each proglottis and lies in large loose coils.

The ovary is fanlike and deeply lobed with a maximum breadth of about 300 μ and lies ventrally in a median position. The vitelline gland, lying immediately posteriorly and slightly porally to the ovary, is irregularly ovoid and measures 104–180 μ × 65–100 μ. The shell-gland, with a diameter of about 15 μ, lies between the ovary and the vitelline gland. On leaving the genital atrium, the vagina lies parallel to the anterior margin and widens out, before reaching the centre of each proglottis, to form a receptaculum seminis.



Figs. 23 and 24. *Raillietina* (*Paroniella*) *siamensis* Schmelz, 1941. Mature proglottis (Fig. 23), and egg with contained oncosphere (Fig. 24).

The uterus can first be seen as a transverse band across the anterior region of the proglottis, and it eventually breaks down to form uterine capsules, each of which contains but one egg. The size of the capsules is 34–38 μ × 30–32 μ; the diameter of the contained eggs (Text-fig. 24) is 25–27 μ × 22–24 μ; and the diameter of the embryos is 9–15 μ. The oncosphere hooks are small, measuring 7–9 μ in length.

Discussion. As can be seen from Table VIII, the present material agrees closely with that described by Schmelz (1941) as *Raillietina* (*Paroniella*) *siamensis* and also with material described by Johnston (1914) as *Davainea sphecotheridis*. Schmelz separated his species from that of Johnston on the following grounds:

(a) *sphecotheridis* is a parasite of Passeriformes whereas *siamensis* is found in Capitoniformes;

(b) The scolex of *sphecotheridis* bears a great number of minute spines, particularly at the base of the rostellum, whereas *siamensis* does not have these;

(c) there are fewer and smaller testes in *sphecotheridis* than in *siamensis*;

(d) the rostellar hooks are smaller in *sphecotheridis*, and there appear also to be differences in the length and breadth of the strobila, in the length of the cirrus-sac and in the diameter of the embryo.

Table VIII

Comparison of Borneo material with *Davainea sphecotheridis* and *Raillietina siamensis*

Species:		*Davainea sphecotheridis*	*Raillietina siamensis*	Borneo material
Strobila: (length × max. breadth in mm.)		100×2	45×4·8–4·9	35×1·15
Scolex (diameter × length in μ)		360	400–440×240	490–525×360
Rostellum (diameter × length in μ)		—	130–150	174–215×85–150
Rostellar hooks	(number)	very great number	240	200–300
	(length in μ)	ant. row: 20 post. row: 15	ant. row: 24 post. row: 20	ant. row: 28 post. row: 19–23
Suckers (diameter in μ)		140	200	174–215×140–178
Sucker spines (length in μ)		up to 10	—	8–18
Testes	(number)	ca. 30	50–60	20–40
	(diameter in μ)	25–30×15–20	80×60	40–90×37–68
Cirrus sac (length × diameter in μ)		100×40	150–160×66–68	90–130×60–74
Ovary (shape and size in μ)		digitiform lobes	495	fanlike, deeply lobed; 300
Vitelline gland (shape and size in μ)		solid and rounded	145	irregularly ovoid 104–180×65–100
Egg capsule (diameter in μ)		27×20 (egg)	30–36	34–38×30–32
Embryo (diameter in μ)		17	12–14	9–15

However, it is clear from the present material that some of these characters which purportedly separate these species are, in fact, common to both. The minute hooks described by Johnston on the scolex of *sphecotheridis* are abundantly clear in the present material but only when the rostellum is not evaginated, which would suggest that they are extremely caducous and which might well explain why Schmelz did not see any such spines, although he was looking for them, in his material. The number of testes in the present material seems to fall half-way between the number described for *sphecotheridis* and the number described for *siamensis*, and it is quite possible that the number of testes is a variable character within the limits quoted. The difference in the sizes of rostellar hooks seems hardly sufficient for this not to be due to measuring technique, particularly in view of the fact that when the hooks of the present material were measured from whole mounts in Canada balsam the lengths were considerably lower than those actually recorded from squash preparations in Berlese fluid.

In view of the number of small discrepancies present between the two species, it may be that they are in fact separate species, but the present material suggests that there is a range of variation which may well encompass both described species. However, without examining the type-material of *sphecotheridis* and that of *siamensis*, it would not be wise to make these two species synonymous and accordingly the present material is tentatively identified as *Raillietina* (*Paroniella*) *siamensis*, as it seems to fit Schmelz's description slightly better than that of Johnston, but it is strongly suggested here that *siamensis* is a synonym of *sphecotheridis*.

It is probable that there is a mistake in labelling in some of the present material as a Charadriiform bird, namely *Charadrius leschenaultii*, is apparently a host for this species, whereas this order of birds has not previously been shown to carry species of *Raillietina* (see discussions following descriptions of *Raillietina* (*R.*) *johri* Ortlepp, 1938 and *Kowalewskiella susanae* n. sp.).

Furthermore, no differences could be found between those worms supposedly from *Charadrius leschenaultii* and those worms from the piciform hosts.

Family **HYMENOLEPIDIDAE** Fuhrmann, 1907

Genus ***HYMENOLEPIS*** Weinland, 1858

Hymenolepis mahonae nom. nov.

(Text-figs. 25–28)

Hymenolepis fringillarum of Mahon, 1958, *nec* Rudolphi, 1810.

HOST. *Aegithina tiphia* 9045.

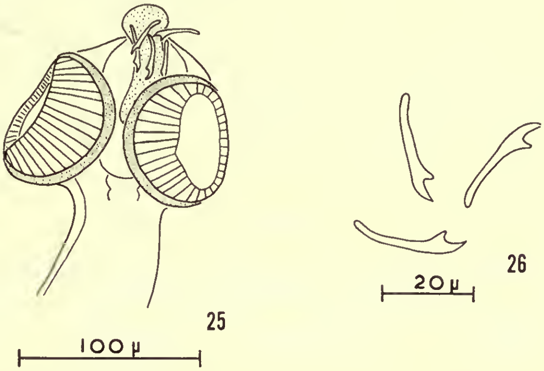
There were several worms present only two of which, however, possessed scolices. Of these two, only one (Text-fig. 25) bore rostellar hooks. The longest complete worm measures 7 mm. and has a maximum diameter of 0·5 mm. There are fragments present, however, where the maximum breadth is almost 0·8 mm. The proglottides are all broader than long, the ratio of breadth to length varying from 3 : 1 to 8 : 1 depending on the part of the worm. The genital apertures are unilateral and the genital ducts pass dorsally to both the ventral and the dorsal excretory vessels.

The scolex is 96 μ long and 140 μ in maximum breadth across the widest part. There are four, apparently unarmed, suckers which measure 62–74 μ × 50–56 μ. The rostellum, 82 μ long by 64 μ in diameter, bears 10 hooks which are 23–28 μ long (Text-fig. 26).

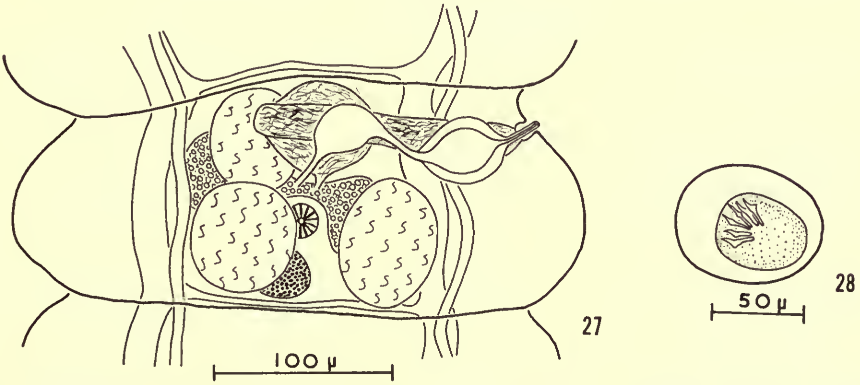
The three testes are arranged in a triangle (Text-fig. 27) with one poral and posterior, one aporal and posterior, and one aporal and anterior. The testes measure 60–65 μ × 49–61 μ. There are both external and internal seminal vesicles. The external seminal vesicle is 25–35 μ in diameter and lies anteriorly about the centre of the proglottis. The internal seminal vesicle is larger and measures 40–50 μ in diameter. The cirrus-sac was not clearly seen, but appears to be about 65–75 μ long by about 40 μ in diameter.

The ovary, bilobed and central, measures up to about 200 μ across its total width, by 50–80 μ. Posterior to the ovary, and lying slightly aporally is the compact vitelline gland which measures 50–55 μ × 36–41 μ. The receptaculum seminis lies prominently in the anterior, median portion of each proglottis and, when full of sperm, reaches a size of 52–70 μ × 48–55 μ.

The present specimens are not sufficiently well preserved to allow the elucidation of details of uterus development. The eggs, however, are 42–48 μ in diameter (Text-fig. 28) while the contained oncospheres are 26–32 μ × 20–30 μ. The hooks of the oncosphere measure 18–20 μ in length.



Figs. 25 and 26. *Hymenolepis mahonae* nom. nov. Scolex (Fig. 25), and rostellar hooks (Fig. 26).



Figs. 27 and 28. *Hymenolepis mahonae* nom. nov. Mature proglottis (Fig. 27), and egg (Fig. 28).

Discussion. The present material agrees well with material described by Mahon (1958) as *Hymenolepis fringillarum* (Rudolphi, 1810). Mahon's description, however, does not agree sufficiently well with the description of Rudolphi (1810), nor with the description of Joyeux and Baer (1936), to allow for its inclusion in the specise *fringillarum*. For purposes of comparison, Mahon includes the figures quoted by Joyeux and Baer in her description, and although the scolex in her material has a diameter of less than half that of the worms described by Joyeux and Baer, and although the cirrus-sac in her material is only a little over half the size of the cirrus sac in the other material, she still identified her material as *H. fringillarum* (see Table IX). It is proposed here that the worms, identified by Mahon as *Hymenolepis fringillarum*, are, in fact, identical with the present material and represent a new species. The new species has been given the patronymic *mahonae* in honour of Dr. June Mahon who first described it. Table X shows all the species of *Hymenolepis* (*sensu lato*), which possess 10 rostellar hooks, so far recorded from Passeriformes and serves to illustrate the differences between the new species and the other existing species. In order to facilitate comparison of the species, it was thought better to retain the generic term *Hymenolepis* (*sensu lato*) despite the work of Spassky and Spasskaja (1954) and Yamaguti (1959) who have sub-divided this vast genus into many smaller genera employing, unfortunately, what in some cases may be regarded as questionable criteria for erecting new genera.

TABLE IX

Hymenolepis fringillarum (Rudolphi, 1810) compared with *H. fringillarum* of Mahon (1958) and present material from Borneo

Species:	*fringillarum* (Rudolphi, 1810)	*fringillarum* (Mahon, 1958, *nec* Rudolphi, 1810)	*mahonae* nom. nov.
Description taken from:	Joyeux & Baer (1936) Lopez- Neyra (1942) Mettrick (1958)	Mahon (1958)	
Strobila (length × max. breadth in mm.)	32–100 × 0·8–1	—	7 × 0·5(0·8)
Scolex (diameter in μ)	210–300	127–145	140
Rostellar hooks (number)	10	10	10
Rostellar hooks (length in μ)	26–28	26	23–28
Suckers (diameter in μ)	90–100 × 100–120	54–58 × 76–79	50–56 × 62–74
Testes (diameter in μ)	150–170	—	49–61 × 60–65
Cirrus sac (length × diameter in μ)	95–110 × 40	54 × 40	65–75 × 40
Eggs (diameter in μ)	57 × 34	—	42–48
Oncospheres (diameter in μ)	48 × 36	—	26–32 × 20–30
Oncosphere hooks (length in μ)	20	—	18–20
Genital apertures (arrangement)	Unilateral	Unilateral	Unilateral

It should be mentioned that Spassky and Spasskaja (1954) transferred *H. fringillarum* to one of their new genera, namely *Passerilepis*, and Yamaguti (1959) lists *fringillarum* as a synonym of *Passerilepis passeris* (Gmelin, 1790). Mettrick (1958), however, redescribed *fringillarum* retaining both the older generic name of *Hymenolepis* and also the specific name of *fringillarum*, but he did not discuss any possible synonymy of this worm. Although there may be valid reasons for retaining both specific names, *fringillarum* (Rudolphi, 1810) is listed in Table X with *passeris* (Gmelin, 1790) in accordance with Ransom (1909) and Yamaguti (1959).

TABLE X

Hymenolepis species with 10 rostellar hooks within the range 23–30μ long from Passeriformes.

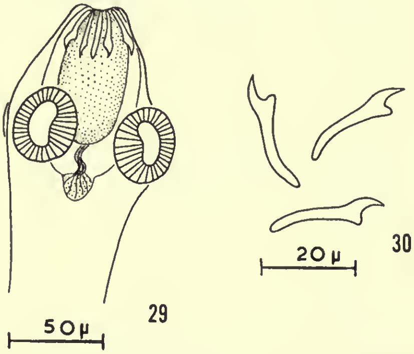
Species:	*farciminosa* (Goeze, 1782)	*hemignathi* (Shipley, 1897)	*magniovata* (Fuhrmann 1918)	*passeris* (Gmelin, 1790) =*fringillarum* (Rudolphi, 1810)	*serpentulus* (Schrank, 1788)	*stylosa* (Rudolphi, 1810)	*zosteropis* (Fuhrmann, 1918)	*mahonae* n. sp.
Description taken from:	López-Neyra (1942*a*/*b*) Mettrick (1958)	Shipley (1897)	López-Neyra (1942*a*/*b*)	Joyeux & Baer (1936) López-Neyra (1942*a*/*b*) Mettrick (1958)	Hughes (1941) López-Neyra (1942*a*/*b*) Mettrick (1958)	Hughes (1941) López-Neyra (1942*a*/*b*) Mettrick (1958)	Hughes (1941)	—
Strobila (length × max. breadth in mm.)	82–120 × 1–1·2	10–22 × 2	25 × 0·4	32–100 × 0·8–1	60–200 × 1·8–2·5	80–110 × 1–1·8	22 × 0·7	7 × 0·5(0·8)
Scolex (diameter in μ)	180–265	—	160	210–300	250–350	200–280	200	140
Rostellum (diameter in μ)	100	—	50	—	50	80–100	—	—
Rostellar hooks (number)	10	10	10	10	10	10	10	10
Rostellar hooks (length in μ)	18–24	18–23	30	26–28	18–27	28–38	30–32	23–28
Suckers (diameter in μ)	85–95	—	70	100–120 × 90–100	75–120	85 × 60	88	62–74 × 50–56
Testes (diameter in μ)	90–100	—	—	150–170	150–200	120–150	—	60–65 × 49–61
Cirrus sac (length × diameter in μ	180–300 × 45	—	100–120 × ?	95–100 × 40	130–190 × 85–110	200–270 × 70–140	120–140 × ?	65–75 × 40
Eggs (diameter in μ)	48–60 × 36–65	40–50	45	57 × 34	110 × 85	—	50–60	42–48
Oncospheres (diameter in μ)	36–48 × 26–30	—	32–36	48 × 36	36–65 × 28–40(20–24)	40–48 × 32–40	23	26–32 × 20–30
Oncosphere hooks (length in μ)	20	20	—	20	20–22	18–20	—	18–20
Avian host (order)	Passeriformes	Passeriformes	Passeriformes	Passeriformes	Passeriformes	Passeriformes	Passeriformes	Passeriformes

***Hymenolepis* sp.**

(Text-figs. 29–32)

HOSTS. *Anthreptes malacensis* 9318, 9358; *Nectarinia calcostetha* 9092.

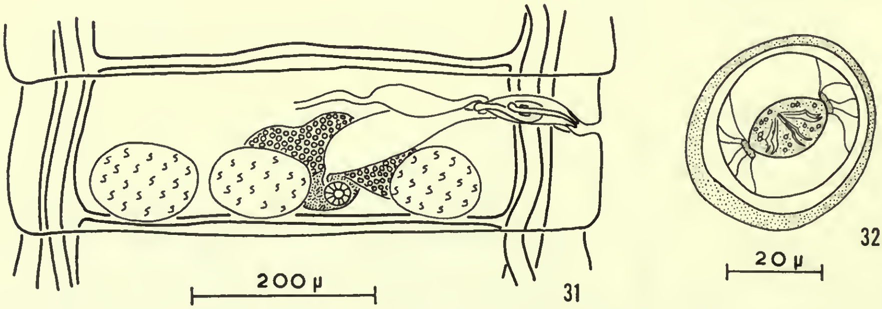
Mature worms measure up to 30 mm. long by 0·35–0·46 mm. in maximum breadth. The genital apertures are irregularly alternating and the genital ducts pass dorsally to both the longitudinal excretory vessels.



FIGS. 29 and 30. *Hymenolepis* sp. Scolex (Fig. 29) and rostellar hooks (Fig. 30).

The scolex (Text-fig. 29) measures 104–121 µ × 115–126 µ and bears an armed rostellum and four, apparently unarmed, suckers. There are 8 hooks (Text-fig. 30) on the rostellum and these measure 28–36 µ long. The suckers are 46–56 µ × 33–49 µ.

The three testes (Text-fig. 31) lie in a straight line and, when mature, measure 64–110 µ × 48–67 µ. The cirrus-sac is 78–88 µ long and has a diameter of 25–33 µ. Although the cirrus was not seen in an extruded position, it could be seen lying within the cirrus-sac and has a diameter of about 6 µ. There is present both an external and an internal seminal vesicle, the latter measuring 21–25 µ × 15–23 µ. The vas deferens is slightly coiled and lies anteriorly to the cirrus-sac, roughly parallel to the anterior edge of the proglottis.



FIGS. 31 and 32. *Hymenolepis* sp. Mature proglottis (Fig. 31), and egg with enclosed oncosphere (Fig. 32).

The ovary is distinctly trilobed and lies in the middle of the proglottis. The vitelline gland, lying immediately posteriorly to the ovary, is compact, measures 65–85 μ × 43–52 μ, and lies ventrally to the middle testis. The receptaculum seminis is large and increases to a maximum size of 163 μ × 80 μ, although in most mature proglottides it measures about 140 μ by about 70 μ.

There is a sudden transition between mature and gravid proglottides, the eggs being only just visible in the last mature proglottis and filling the whole of the medulla, extending beyond the excretory vessels, in the first gravid proglottis. The eggs (Text-fig. 32) measure 25–40 μ in diameter and the contained oncospheres are 10–14 μ in diameter. The hooks of the oncosphere are 7–9 μ long.

DISCUSSION. The present material does not resemble any species listed by Fuhrmann (1932), Lopez-Neyra (1942*a*, *b*), or by Yamaguti (1959) as coming from Passeriformes. However, in view of the fact that it has not been possible to examine all the references to *Hymenolepis* (*sensu lato*) it was considered advisable not to erect a new species to contain this worm at this time.

Genus ***FIMBRIARIA*** Frölich, 1802

Fimbriaria fasciolaris (Pallas, 1781)

HOST. Domestic duck (*Anas boschas* L. *dom.*) 9575.

Specimens are greatly contracted, but appear to fit the description by Wolffhügel (1936), who also lists the full synonymy of this species. Webster (1943*a*), in his review of the Fimbriariinae, mentions that he found a smaller range in the number of longitudinal muscle-bundles in *F. fasciolaris* than is quoted by Wolffhügel, the former finding only 110–120 in his material whereas Wolffhügel gives the range as 60–120. Although the present material is not well enough preserved for any description, its similarity both to the worms described by Wolffhügel (1936) and to specimens in the Helminthological collection of the British Museum (Natural History) identified as *Fimbriaria fasciolaris* makes identification reasonably positive.

Family **DILEPIDIDAE** Fuhrmann, 1907

Genus ***PARICTEROTAENIA*** Fuhrmann, 1932

Paricterotaenia burti Sandeman, 1959

(Text-fig. 33)

HOST. *Charadrius leschenaultii* 9110.

One, small immature worm was present which measured 0·35 mm. long by 0·12 mm. in maximum breadth. Only two immature proglottides were present, both being twice as broad as long.

The scolex (Text-fig. 33) is 200 μ × 240 μ and possesses four unarmed suckers, 120–140 μ × 100–110 μ. The rostellum, 150 μ long by 70 μ in diameter, bears 16 hooks arranged in what appears to be a single row. The hooks are 50–52 μ long. No genitalia were seen at all.

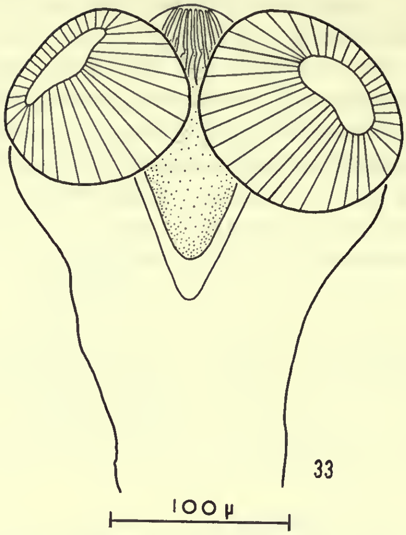


FIG. 33. *Paricterotaenia burti* Sandeman, 1959. Scolex.

DISCUSSION. The present material appears to agree sufficiently well with *Paricterotaenia burti* Sandeman to warrant identification with that species. Sandeman (1959*a*) erected the species to contain worms he found in *Lymnocryptes minimus* and *Numenius arquatus* from the River Eden, Fife, and also to contain, in part, *Paricterotaenia stellifera* (Krabbe, 1869). In the original description of *P. stellifera* Krabbe gives two sets of hook characteristics: one with 10 hooks, 55 μ long; and the other with 14 hooks of length 46–51 μ. The former set of hook characters is that which has become ascribed to *P. stellifera* (Krabbe, 1869) while the latter, prior to Sandeman, had been ignored. Hooks of the present material agree closely with those drawn and described by Krabbe and also those described by Sandeman which pertain to *P. burti*. The measurements of the scolex and rostellum also agree reasonably closely with Sandeman's description and, furthermore, the worm described by Krabbe, by Sandeman, and the present worm were all found in Charadriiformes. This appears to be the first record of this worm in Asia.

Genus *DILEPIS* Weinland, 1858

Dilepis ardeolae Singh, 1952 (?)

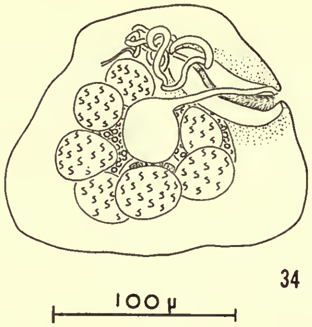
(Text-fig. 34)

HOST. *Butorides striatus* 9040.

The worms are small, measuring up to about 3 mm. long by 0·25 mm. in maximum breadth. The genital apertures are unilateral.

The scolices are all missing, although several worms are present.

There are 7 testes (Text-fig. 34) lying mainly posteriorly and dorsally to the female genitalia and measuring 30–40 μ in diameter. In some proglottides, the testes can be seen extending laterally and anteriorly to the ovary on the aporal side. Neither an internal nor an external seminal vesicle was seen. The cirrus-sac,



34

FIG. 34. *Dilepis ardeolae* Singh, 1952 (?) Mature proglottis.

though not seen clearly, appears to measure about 80 μ long by about 25 μ in diameter, but this is probably a low figure as there were no gravid proglottides present for comparison. The cirrus is armed, but was not seen in the extruded position. In the anterior region of maturing proglottides, the vas deferens becomes profusely coiled and probably serves as an external seminal vesicle when it swells up with sperm.

Lying approximately in the middle of the proglottis is the bilobed ovary, each lobe tending to be more or less spherical. The vitelline gland, lying immediately posteriorly to the ovary, is compact and measures about 30 μ × 20 μ. In the majority of cases, the vagina opens into the genital atrium posteriorly to the opening of the cirrus-sac, but this is not constant. Towards the centre of the proglottis the vagina opens into a receptaculum seminis which is broadly fusiform.

DISCUSSION. The only feature in which the present material differs from that described by Singh (1952) as *Dilepis ardeolae* is the size of the cirrus-sac. In Singh's material the length of the cirrus-sac is given as 0·248–0·31 mm. and the diameter as 0·031–0·037 mm. The cirrus-sac in the present material, however, appears to be much smaller, being only about 80 μ long by 25 μ in diameter, but as there are no gravid proglottides present it is difficult to state whether the size of cirrus-sac measured is the largest size in a complete worm. Despite the apparent discrepancy in size of cirrus-sac, the other characters are in such close agreement that the present worms are tentatively identified as *Dilepis ardeolae* Singh, 1952. Moreover, the fact that the host *Ardeola grayi* from which Singh described his species, is closely related both in habitat and phylogenetically to *Butorides striatus*, the host from which the present material comes, further suggests that the worms may be of the same species.

Genus ***LIGA*** Weinland, 1857

Liga facile (Meggitt, 1927) Szpotanska, 1931

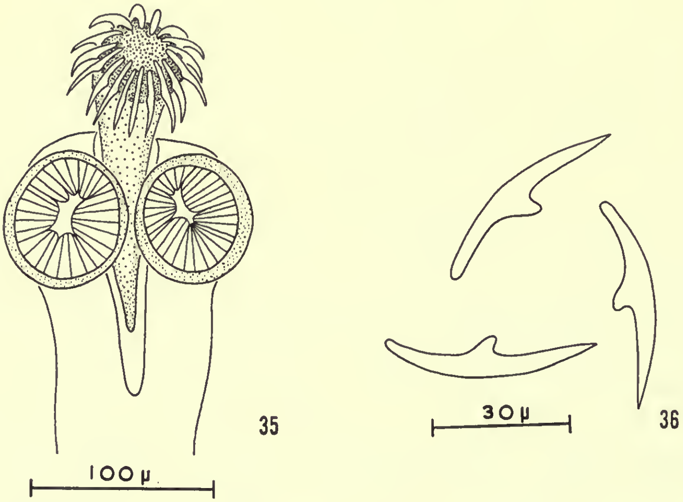
(Text-figs. 35–36)

Anomotaenia facile Meggitt, 1927.
Anomotaenia trivialis Meggitt, 1927.

HOST. *Actitis hypoleucos* 9196.

The worms are very small, not exceeding 1 mm. in length, and without exception are immature, no genitalia being seen at all. The maximum breadth in all the worms present is the breadth of the scolex across the region of the suckers, as in no instance does the breadth of any of the proglottides exceed the breadth of the scolex.

The scolex (Text-fig. 35), including the rostellum, measures 160–170 μ in length and is 130–150 μ broad. The suckers measure 79–82 μ × 72–76 μ and are unarmed. There are, however, some marks which may be the scars of attachment of acetabular spines along the posterior edge of the suckers. The rostellum, measuring 80–100 μ long by 40–60 μ in diameter, bears 20 hooks in two alternating rows. The hooks (Text-fig. 36) in each row are of different sizes: those lying posteriorly measure 41–43 μ long, while those lying anteriorly measure 46–51 μ long.



FIGS. 35 and 36. *Liga facile* (Meggitt, 1927). Scolex (Fig. 35) and rostellar (hooks Fig. 36).

DISCUSSION. The present material differs only slightly from that described by Meggitt (1927*b*) in that the scolex of Meggitt's material is 270 μ × 290 μ, whereas the scolex in the present material is 130–150 μ × 160–170 μ. In view of the close correlation, however, which obtains in the number and size of the rostellar hooks, the size of the rostellum, the small size of the whole worm; and, furthermore, in the fact that both worms are parasites of wading birds, it seems reasonable to identify the present material as *Liga facile* (Meggitt, 1927).

Szpotanska (1931) reviewed the genus *Liga* Weinland, 1857, and transferred *Anomotaenia facile* Meggitt, 1927, and *A. trivialis* Meggitt, 1927, to this genus. She regarded *trivialis* as a synonym of *facile* and redescribed the latter species using new material from *Burhinus oedicnemus*. Sandeman (1959*a*), while accepting that both species belong to the genus *Liga*, nevertheless regards *facile* and *trivialis* as distinct species, but has not yet published his evidence for this view. Williams (1962), however, having examined the type-material of both *facile* and *trivialis*, supports the view of Szpotanska that the two species are not distinct. On the basis of his comparison of Meggitt's type-material with the descriptions of both Meggitt and Szpotanska, he states, in his detailed review of the genus *Liga*, that there seems to be " scant evidence for regarding *A. facile* and *A. trivialis* as distinct species ". The main feature of difference between *facile* and *trivialis* from Meggitt's description is the size of the rostellar hooks. In *A. facile* the hooks are 40–50 μ long, while in *A. trivialis* the hooks are 38–39 μ long. As can be seen in the present material, however, the hooks in the anterior row are longer than those in the posterior row. Accordingly, it is not improbable that Meggitt measured hooks from both rows in the material he described as *A. facile*, but measured only hooks in the posterior row in the material he described as *A. trivialis*. The fact that Williams (1962), on re-examining the type-specimens of *A. trivialis*, found hooks as long as 45 μ supports this postulation. Therefore, there appears to be no justification for regarding *facile* and *trivialis* as distinct species.

Genus ***ANOMOTAENIA*** Cohn, 1900

Anomotaenia depressa (Siebold, 1836) Fuhrmann, 1908

(Text-figs. 37–39)

Taenia depressa Siebold, 1836.
Liga frigida (Meggitt, 1927).

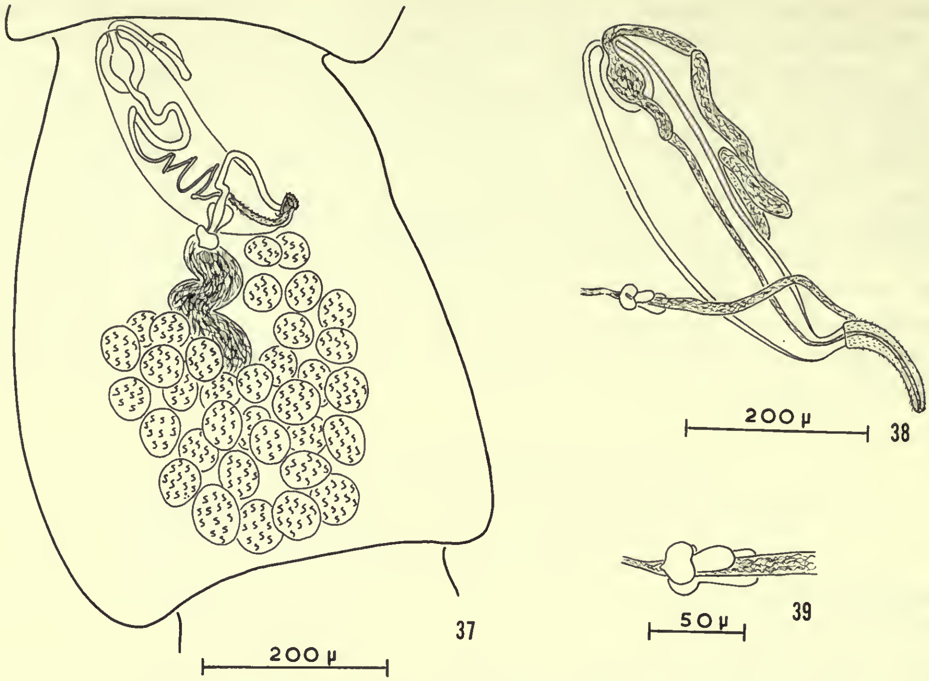
HOST. *Apus affinis* 8784.

The present material comprises fragments, all of which probably come from a single worm. The total length of all the fragments is 8 mm. and the maximum breadth is 0·6 mm. The immature proglottides at first tend to be rather square in shape, but as they mature they become longer than broad. The genital apertures are irregularly alternating.

The scolex is missing.

There are 30–40 testes (Text-fig. 37) which surround the female genitalia laterally and posteriorly and which measure 40–70 μ in diameter. The cirrus-sac (Text-fig. 38) is large, with a length of 400–480 μ and a diameter of 80–100 μ. The cirrus appears to be fairly short when extruded, having a maximum observed length of 150 μ. The diameter of the cirrus base is about 30 μ and the diameter of the tip is 12 μ. The cirrus is covered for most of its length with fine spines about 4–5 μ long. There is no external seminal vesicle present, but the vas deferens, on entering the cirrus-sac, expands to form an internal seminal vesicle in the proximal part of that organ. The ductus ejaculatorius is quite narrow and lies convoluted in the distal part of the cirrus-sac before entering the cirrus.

The deeply-lobed ovary is situated posteriorly and ventrally to the cirrus-sac which, in some proglottides, overlies part of the ovary. The vitelline gland, lying posteriorly to the ovary and anteriorly to the testes, is irregularly lobular. The vagina has its opening into the genital atrium posterior to that of the cirrus-sac and lies parallel to the cirrus-sac until it eventually leads into the receptaculum seminis through a peculiar, " chitinoid " structure (Text-fig. 39). This structure is roughly dumb-bell shaped and has a length of 55–57 μ. The diameter of the part



Figs. 37–39. *Anomotaenia depressa* (Siebold, 1836). Mature proglottis showing male genitalia and vagina (Fig. 37), cirrus-sac and part of the vagina (Fig. 38), and chitinoid vaginal apparatus (Fig. 39).

closest to the vagina is the same as the diameter of the part next to the receptaculum seminis and measures 27–29 μ. The diameter of the narrow constriction is 8–10 μ. The receptaculum seminis, situated immediately behind the cirrus-sac and dorsal to the vitelline gland, has a twist in it and when filled with sperm reaches up to 100 μ in overall length by about 40 μ in diameter.

Gravid proglottides are not present.

Discussion. Although the scolex is missing and gravid proglottides are not present, this worm is almost certainly the same species as that described by Joyeux and Baer (1936) from *Apus apus*. Through the kindness of Professor J. G. Baer, I have had a chance to compare the above material with worms from his own collection which he had identified as *Anomotaenia depressa* and undoubtedly the worms were identical.

The " chitinoid " structure present at the junction of the vagina and the receptaculum seminis was described by Joyeux and Baer (1936) thus: " Le vagin est entouré, près du réceptacle séminal, d'un manchon cellulaire, auquel fait suite un appareil de fermeture chitineaux, à l'entrée de ce réceptacle." In order to measure the structure in the present material accurately, two proglottides were mounted, unstained, in Berlese fluid which rendered most of the tissue transparent. Those structures which showed to advantage after this treatment were the cirrus-sac, the narrow portion of the ductus ejaculatorius, the cirrus with its armature of spines, and the structure surrounding the vagina as it enters the receptaculum seminis.

Dollfus (1958, p. 515), in a footnote, suggests that the structure may be made of a scleroprotein, but that its chemical nature is not known. In the same paper Dollfus reviews those species belonging to the genera *Anomotaenia* Cohn, 1900; *Pseudangularia* Burt, 1938(*a*); *Neoangularia* Singh, 1952; and *Neoliga* Singh, 1952; which possess this structure which he describes as " un appareil occlusif entre le réceptacle séminal et le vagin distal ".

Dollfus (1958) discusses fully the complicated synonymy of *Anomotaenia depressa* (Siebold, 1836) and cites all the descriptions of note. Most of these descriptions are inadequate on their own, and accordingly Dollfus gives a compound description which takes into account those given by Krabbe (1869), von Linstow (1897), Fuhrmann (1899*a*), López-Neyra (1923), Joyeux and Timon-David (1934) and which agrees with data taken from his own material. In the résumé of his paper Dollfus stresses the insufficiency of present knowledge of both *Anomotaenia depressa* (Siebold, 1836) and *A. cyathiformis* (Frölich, 1791), particularly as both these species have been described both from Passeriformes and Cypseliformes. Furthermore, several authors have used, for descriptions of *cyathiformis*, characters of worms taken from hosts belonging to both these orders. A more recent, though short, description of *A. depressa*, which agrees with that of Joyeux and Baer (1936), is given by Vojtechovska-Mayerova (1952).

Anomotaenia nymphaea (Schrank, 1790)

(Text-figs. 40–41)

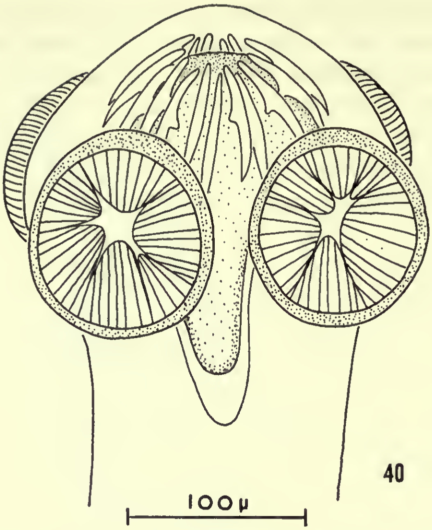
Taenia nymphaea Schrank, 1790

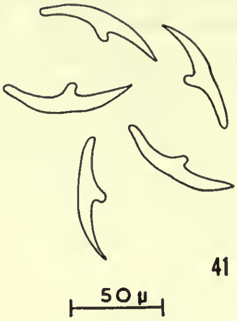
HOST. *Numenius phaeopus* 9530.

Two, small immature worms only were present. Both had complete scolices with full complements of rostellar hooks. A squash preparation was made of one of the scolices while the other was mounted whole in Canada-balsam.

The longer of the two worms measures 0·75 mm. with a maximum breadth of 0·11 mm. The scolex (Text-fig. 40) is 200 μ long, including the length of the rostellar sac, and has a diameter of 250 μ. The suckers are ovoid and measure 90–110 μ × 80–90 μ. No sucker spines were seen. The rostellum is invaginated, measures 200 μ from its tip to the posterior extremity of the rostellar sac by 110 μ across the broadest part, and carries 20–22 hooks arranged in a double row. The rostellar hooks (Text-fig. 41) are of two sizes, the larger, lying anteriorly, are 75-80 μ long, while those in the posterior row are 65–70 μ long.

DISCUSSION. The present material agrees well with material described by Joyeux and Baer (1936) and by Mahon (1958), although Mahon's material was probably in a greater state of relaxation than the present, as the diameter of the suckers in her material is considerably greater. Sandeman (1959*a*) has so far been unable to deal with the synonymy of this species, but is at present working on this.





FIGS. 40 and 41. *Anomotaenia nymphaea* (Schrank, 1790). Scolex (Fig. 40) and rostellar hooks (Fig. 41).

Anomotaenia tringae (Burt, 1940) Sandeman, 1959

(Text-figs. 42–43)

Paricterotaenia tringae Burt, 1940.
Anomotaenia paramicrorhyncha Dubinina, 1953.

HOST. *Tringa glareola* 9255.

The worms measure up to 16 mm. long by 0·73 mm. in maximum breadth. In immature proglottides the breadth is about twice the length, but as the proglottides mature and become gravid, so does the ratio of length to breadth increase until in the gravid proglottides the length is about equal to the breadth. The genital apertures are 89 % regularly alternating. The genital ducts pass between the dorsal and ventral excretory vessels.

Scolices are not present.

There are 9–11 testes (Text-fig. 42), most of which lie aporally, and they measure 45–70 μ × 25–40 μ. There does not appear to be either an internal nor an external seminal vesicle. The cirrus-sac measures 87–100 μ long by 25–35 μ in diameter and has a typical constriction about halfway along its length. In many instances the unarmed cirrus could be seen projecting into the vagina.

The ovary is irregularly digitate, lies in the anterior third of mature proglottides, and stretches from the aporal excretory vessels almost to the poral excretory vessels. The slightly lobular vitelline gland lies posteriorly to the ovary, but in front of the testes, and measures 45–75 μ across. Lying to the poral side of the vitelline gland is the receptaculum seminis which is ovoid and measures 59–74 μ × 46–64 μ when not swollen with sperm, but when swollen reaches up to 130 μ × 70 μ.

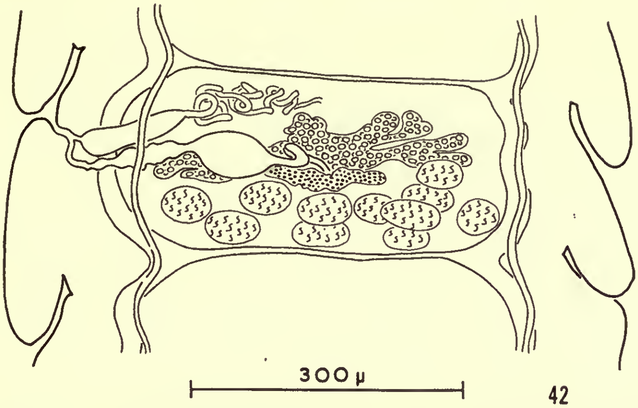


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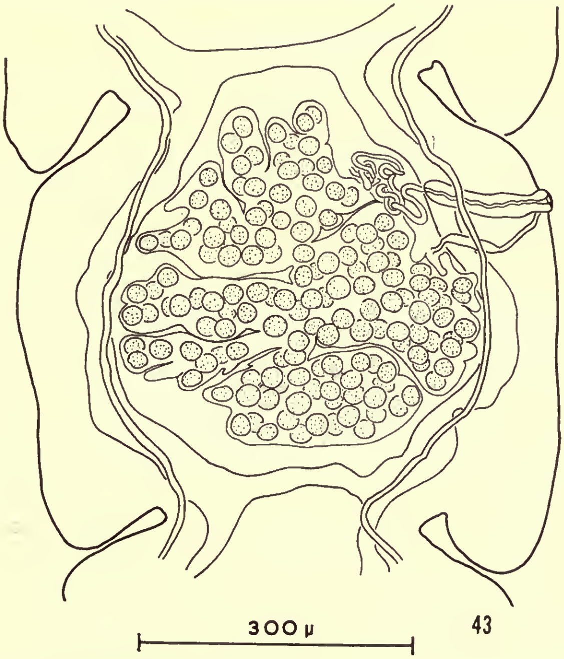
Fig. 42. *Anomotaenia tringae* (Burt, 1940). Mature proglottis.



43

Fig. 43. *Anomotaenia tringae* (Burt, 1940). Gravid proglottis.

The uterus is sac-shaped initially, becomes increasingly lobular as the eggs ripen (Text-fig. 43), until in fully-gravid proglottides it tends to break down into pseudo uterine capsules. The eggs measure 34–39 µ × 31–34 µ and the contained oncospheres are 25–30 µ × 24–25 µ. The hooks of the oncosphere were not fully formed.

Discussion. The present material agrees well with the type-material of *Paricterotaenia tringae* which Mr. D. R. R. Burt has so kindly placed at my disposal, and with material described by Baer (1959). Despite the fact that the scolex is wanting in the present material, such good correlation obtains through direct comparison of the rest of the anatomy with the type-material, that there remains no doubt as to the identity of the present worms. Sandeman, (1959*a*) transfers this species from the genus *Paricterotaenia* to the genus *Anomotaenia*. Burt (1940) states that owing to the fact that there does not exist a dilepid genus with a double crown of hooks and regularly alternating genital apertures " The choice lies therefore between *Anomotaenia* and *Paricterotaenia* ". Burt chose to place the species in the genus *Paricterotaenia* on the grounds that the scolex and rostellum are very similar to those seen in several species of *Paricterotaenia*. The transference of this species to *Anomotaenia* by Sandeman appears to be purely on the grounds of its possessing a double row of hooks and this is accepted by Baer (1959). Until such a time as Sandeman publishes his larger work on the dilepids of waders, and explains his justification for such a treatment, it is probably best to leave this species in the genus *Anomotaenia*.

Genus ***PARVITAENIA*** Burt, 1940

Parvitaenia sp.

(Text-fig. 44)

HOST. *Butorides striatus* 9040.

The worm is incomplete, lacking a scolex. It measures 14 mm. in length by 0·9 mm. in maximum breadth. The proglottides are all broader than long and the genital apertures are irregularly alternating.

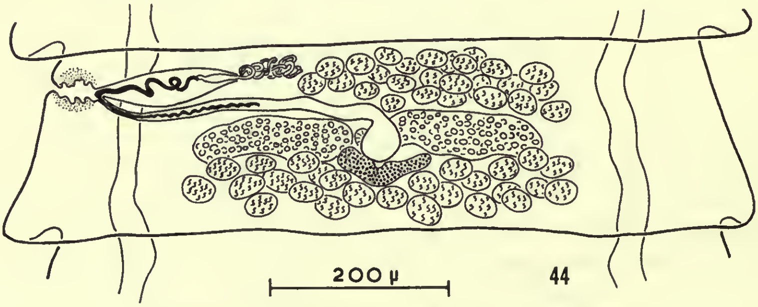


FIG. 44. *Parvitaenia* sp. Mature proglottis.

There are 50–52 testes (Text-fig. 44), half lying anteriorly to the female genitalia and half lying posteriorly, which measure 30–50 μ × 15–45 μ. The cirrus-sac is not distinct, but appears to be about 115 μ long and 45 μ in diameter. It lies close to the anterior margin of the proglottis, opening into the genital atrium on the lateral margin. The cirrus is long and in many cases can be seen projecting into the vagina of the same proglottis and reaching almost to the receptaculum seminis.

The ovary is distinctly bilobed, the combined length of both lobes measuring 345–395 μ. The vitelline gland, lying more or less in the centre of the proglottis and posterior to the ovary, is irregularly bilobed having a width of 90–110 μ. Lying between the ovary and the vitelline gland is the roughly spherical shell-gland which has a diameter of about 45 μ.

There are no gravid proglottides, but in the most mature of those present eggs can be seen accumulating in the anterior poral part of each proglottis. The parenchyma contains many calcareous corpuscles.

DISCUSSION. It is not possible to identify this material as to species owing to the lack of a scolex. The internal anatomy, however, strongly suggests that it belongs to the genus *Parvitaenia* Burt, 1940. Baer and Bona (1960) slightly alter Burt's generic diagnosis and consider the genus to contain 13 valid species: *P. ardeolae* Burt, 1940; *P. macropeos* (Wedl, 1855); *P. cochlearii* Coil, 1955*a*; *P. purpurea* Johri, 1959; *P. magna* Baer, 1959; *P. macrophallica* Baer and Bona, 1960; *P. microphallica* Baer and Bona, 1960; *P. ambigua* Baer and Bona, 1960; *P. ardeae* (Johnston, 1911); *P. glandularis* (Fuhrmann, 1905); *P. aurita* (Rudolphi, 1819); *P. clavipera* Baer and Bona, 1960; and *P. pseudocyclorchida* Baer and Bona, 1960. Of these, five are new species and four are new combinations. The full descriptions of the new species are to be given at a later date and, until such time as these descriptions appear, simply allocating the present material to the genus *Parvitaenia* should suffice.

Genus ***VITTA*** Burt, 1938

Vitta rustica (Neslobinsky, 1911) Baer, 1959

(Text-figs. 45–46)

Anomotaenia rustica Neslobinsky, 1911.
Vitta magniuncinata Burt, 1938.

HOST. *Hirundo rustica* 9202.

The strobila measures 25 mm. long by 2·5 mm. in maximum breadth. The proglottides are all broader than long, the ratio of breadth to length varying from 3 : 1 to 5 : 1 depending both on the state of contraction of the worm and on the site of the proglottis within the strobila. The genital apertures are irregularly alternating and situated laterally, close to the anterior margin of each proglottis, while the genital ducts pass dorsally to both the ventral and dorsal excretory vessels.

The scolex (Text-fig. 45) has a diameter of 370 μ and a length, including the length of the rostellum, of 330 μ. The suckers are 73–81 $\mu \times$ 67–79 μ and are unarmed. The rostellum, 185 μ long by 165 μ in diameter, bears 42–45 hooks arranged in two rows in such a way that for every one hook in the anterior row, there are two hooks in the posterior row. The hooks are 50–60 μ long, those hooks in the posterior row being slightly longer than those of the anterior row.

There are 60–90 testes (Text-fig. 46) which, when fully developed, measure 62–77 $\mu \times$ 60–67 μ, and which are arranged posteriorly and laterally to the vitelline gland and dorsally to the ovary. There is no external seminal vesicle as such, but the vas deferens expands in the region of the cirrus-sac and lies in large loose coils which function as an external seminal vesicle. On entering the cirrus-sac, the vas deferens forms an internal seminal vesicle. The cirrus-sac, lying parallel and close to the anterior margin of the proglottis, measures 320–360 μ long by 65–85 μ in diameter.

The ovary is bilobed, each lobe being fan-like and divided into a great number of smaller lobes which reach the excretory vessels on both sides of the proglottis.

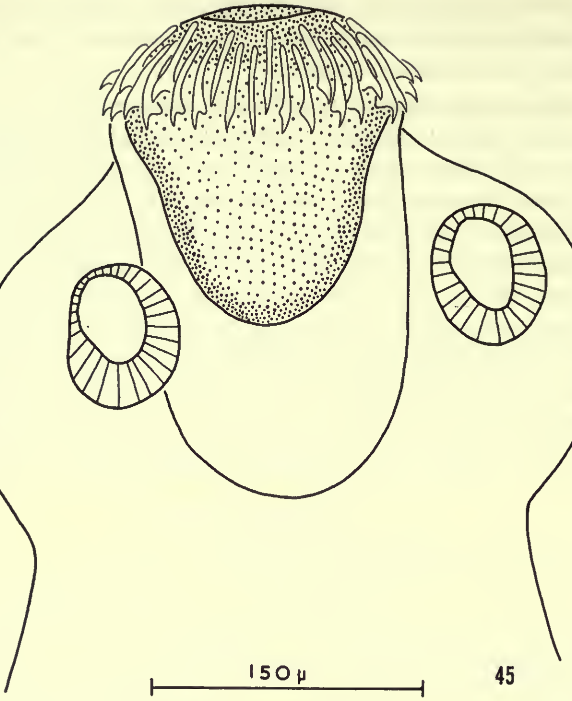


FIG. 45. *Vitta rustica* (Neslobinsky, 1911). Scolex.

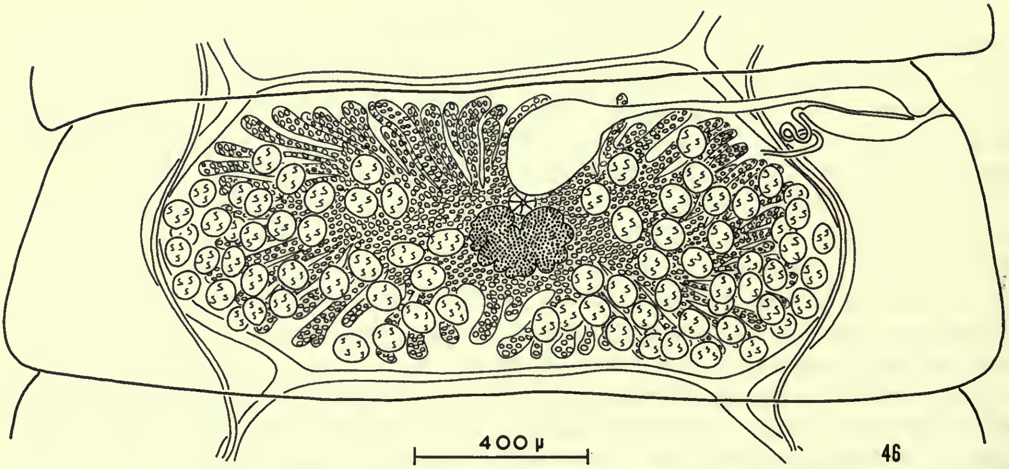


FIG. 46. *Vitta rustica* (Neslobinsky, 1911). Mature proglottis.

The vitelline gland is U-shaped and measures 90–110 µ × 50–70 µ. Situated dorsally and slightly anteriorly to the vitelline gland is a well-defined shell-gland, 45 µ in diameter. In the more mature proglottides, the receptaculum becomes quite swollen, often exceeding the size of the cirrus-sac.

DISCUSSION. The above material agrees well with that described by Burt (1938*b*) as *Vitta magniuncinata* and with that described by Baer (1959) as *V. rustica*. The genus *Vitta* was erected by Burt (1938*b*) to contain two different worms taken from *Hirundo rustica gutteralis* Scop., 1786, namely *magniuncinata* and *minutiuncinata*. The genus closely resembles *Anomotaenia* Cohn, the main feature of difference being that in *Anomotaenia* the genital ducts pass between the excretory vessels, whereas in *Vitta* they pass dorsal to both. Baer (1959) transfers *Anomotaenia rustica* Neslobinsky, 1911, to the genus *Vitta* and places *magniuncinata* as a synonym of *rustica*. He also provides a key to the four species of *Vitta* which he recognizes, using only the characters of hook number and size, and number of testes. These four valid species are: *V. parvirostris* (Krabbe, 1869); *V. minutiuncinata* Burt, 1938; *V. undulatoides* (Fuhrmann, 1908*b*); and *V. rustica* (Neslobinsky, 1911).

Yamaguti (1959) includes *Vitta* as a synonym of *Angularella* Strand, 1928, but gives no indication as to what grounds he has for this. The diagnostic characters of the genera differ essentially in the arrangement of the rostellar hooks. In *Vitta* there is a double row, whereas in *Angularella* there is a single row. On this basis, it is proposed to retain, as valid, the genus *Vitta* Burt, 1938.

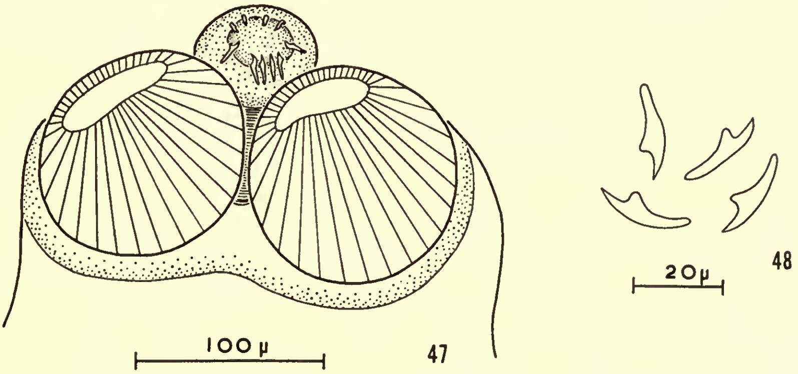
Dilepidid sp.

(Text-figs. 47–48)

HOST. *Cacomantis merulinus* 9503.

The strobila measures 3·5 mm. long by 0·7 mm. in maximum breadth. The genital apertures are unilateral. The worm is in a poor state of preservation and did not stain well.

The scolex (Text-fig. 47) is 160 μ long, including the length of the rostellum, by 260 μ broad across the suckers. The four suckers are circular in outline and measure 100–110 μ in diameter. Sucker spines were not seen. The rostellum, 65 μ long and 45 μ in diameter, bears a single row of 10 hooks which are not evenly spaced round the periphery therefore suggesting that there may have been some hooks lost. The length of the hooks is 18–19 μ and their shape can best be seen in Text-fig. 48.



FIGS. 47 and 48. Dilepidid. Scolex (Fig. 47), and rostellar hooks (Fig. 48).

The only genitalia that can be made out with any certainty are the testes, which number 24–30, and which measure 45–75 μ × 23–38 μ. In one segment there was a suggestion of double genitalia, but this clearly was not the normal arrangement.

DISCUSSION. The worms show many features of the Dilepididae, but could belong to a wide range of genera. But for the shape of hooks, the data available from this worm agree very closely with those of *Anomotaenia mutabilis* (Rudolphi, 1819) Fuhrmann, 1907, even as to the order of host it infests. Owing to the lack of mature and gravid proglottides which can be described, identification further than the family is not possible.

Genus ***KOWALEWSKIELLA*** Baczynska, 1914

Kowalewskiella susanae n. sp.

(Text-fig. 49)

HOST. *Tringa glareola* 9255.

Several worms are present in a good state of preservation. They measure up to 25 mm. long by 0·525 mm. in maximum breadth. The immature proglottides are slightly broader than long, but the mature proglottides become twice as long as they are broad. The genital apertures are irregularly alternating. The genital ducts pass between the dorsal and ventral excretory vessels.

The scolex measures 90–100 μ in diameter, but is bent and squashed so that the length cannot be measured accurately. The suckers are about 45 μ in diameter, but these too are squashed. Only three hooks were seen on the rostellum, of which only one could be measured, its length being about 8 μ.

There are 21–30 testes (Text-fig. 49) arranged in two groups, one group lying anteriorly to the female genitalia and the other lying posteriorly. The number of testes in each group is approximately equal and the size of the testes is subject to wide variation measuring 45–65 μ × 35–60 μ. There is neither an internal nor an external seminal vesicle present, the vas deferens, however, probably acts as an external seminal vesicle as it becomes greatly swollen with sperm in mature proglottides. The cirrus-sac is 92–98 μ long by 53–60 μ in diameter and is situated laterally, in about the middle of the proglottis. It opens into a well-developed genital atrium. In the mounted material, the cirrus is present only as a short papilla, but there is a convoluted ductus ejaculatorius still present in the cirrus-sac.

The ovary is distinctly bilobed, each lobe being separated by a relatively long isthmus. The lobes are irregularly lobular and, in proglottides where the cirrus-sac is well developed, the total breadth of the ovary is 150–250 μ. The vitelline gland, lying posteriorly to the ovary, measures 55–90 μ × 34–52 μ. Just in front of the vitelline gland, but dorsal to it and behind the ovary, is the shell-gland which has a diameter of 20–25 μ. The receptaculum seminis lies between the cirrus-sac and the ovary and shows wide variation in size depending on the quantity of sperm present, the normal variation being 60–90 μ × 40–50 μ.

Gravid proglottides were not found.

British Museum (N.H.) Reg. no. 1968.4.25.47–48.

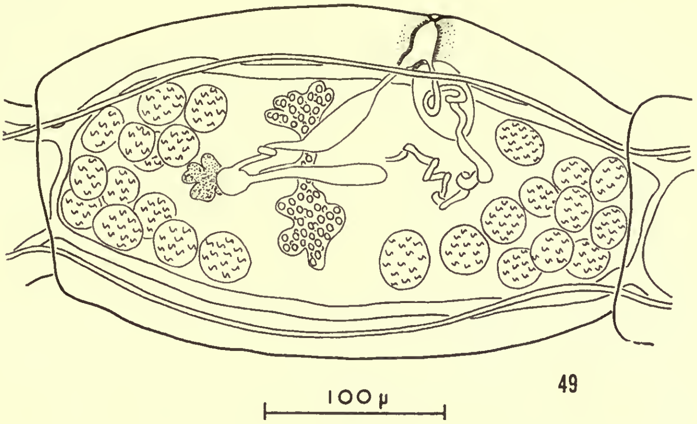


FIG. 49. *Kowalewskiella susanae* n. sp. Mature proglottis.

DISCUSSION. The present material agrees well with material from the same host described by Baer (1959) as *Kowalewskiella cingulifera* (Krabbe, 1869) Sandeman, 1959. Sandeman (1959*a*) re-erects the genus *Kowalewskiella* Baczynska, 1914, to contain all those species in which the testes are divided into two groups, one anterior to the female genitalia, and the other posterior. In accordance with this, he transfers *Choanotaenia glareolae* Burt, 1940, *Choanotaenia stagnatilidis* Burt, 1940, and *Choanotaenia hypoleucia* [*sic*] Singh, 1952, all to the genus *Kowalewskiella*. Furthermore despite the differences apparently inherent between these species and Krabbe's, species *cingulifera*, he regards them all, as well as *Kowalewskiella longiannulata* Bacyznska, 1914, as synonyms of *cingulifera*. Baer (1959) accepts this view and in a personal communication points out that " *K. cingulifera* forms a group within which variations appear to be considerable ". This assumption is presumably based on the fact that Baer (1959) described some worms from *Tringa glareola*, from the Belgian Congo, as *K. cingulifera*. As can be seen from the accompanying table (Table XI) if Baer's material is, in fact, *cingulifera* then there would be present very great variation within the species; more variation than can readily be accepted as existing in any one species. If the two species of Burt (1940), the species described by Singh (1952) and that of Baczynska (1914), are also considered as *cingulifera*, then this increases the already wide variation even more. Sandeman (1959*a*) does not outline his reasons for placing these various worms in synonymy with *cingulifera*, but it is doubtful if this sweeping treatment is justified in the present circumstances and, accordingly, it is here suggested that *cingulifera*, *longiannulata*, *glareolae*, *stagnatilidis* and *hypoleuca* are all separate species.

To these five valid species should also be added *Kowalewskiella bodkini* (Vevers, 1923) n. comb. (= *Raillietina* (*Skrjabinia*) *bodkini* Vevers, 1923), *K. buzzardia* Tubangui and Masiluñgan, 1937, and *K. susanae* n. sp. It is unfortunate that Krabbe's original description is not more complete, but it can be differentiated from any of the others on the large size of the scolex, and on the large number of rostellar hooks. *K. longiannulata* can be distinguished from the rest by the fact that it has a

TABLE XI

Comparison of known species of *Kowalewskiella* with *K. susanae* n. sp. from Borneo.

Species:	*cingulifera* (Krabbe, 1869)	*longiannulata* (Baczynska, 1914)	*glareolae* (Burt, 1940)	*stagnatilidis* (Burt, 1940)	*hypoleucia* (Singh, 1952)	*bodkini* (Vevers, 1923)	*bodkini* (Vevers, 1923)	*buzzardia* (Tubangui & Masiluñgan, 1937)	*cingulifera* (Baer, 1959, *nec* Krabbe, 1869)	*susanae* n. sp.
Descriptions taken from:	Krabbe (1869)	Baczynska (1914)	Burt (1940)	Burt (1940)	Singh (1952)	Vevers (1923)	Personal measurements of co-type material	Tubangui & Masiluñgan (1937)	Baer (1959)	
Strobila (length × max. breadth in mm.)	100 × 1	30–40 × 0·54	39–41 × 0·66–0·83	70–120 × 1·15–1·3	35–40 × 0·42–0·46	50 × ?	38–48 × 1·2	160 × 1·9	35 × 0·57	25 × 0·525
Scolex (diameter in μ)	—	65	95	98–100	480–630 (=48–63?)	135	108–136	400	91	90–100
Rostellum (diameter in μ)	—	3·9 (=39?)	37–46	41	43–56	50	48–55	130	—	—
Rostellar hook (number)	ca. 40	28–30	36–40 (calculated)	28	26	36	—	10	30	—
Rostellar hook (length in μ)	4–5	52–60 (=5·2–6·0?)	7	6	6–7	6	—	61–65	8–9	8
Suckers (diameter in μ)	—	23	27–35	37	43–52	50	30–55	120	41	45
Testes (number)	—	ca. 52	30–40	50–62	35–50	45–50	35–54	30	21–31	21–30
Cirrus sac (length × diameter in μ)	—	93·6 × 46·8	188–222 × 62–70	170–204 × 48–60	215–279 × 64–73	(120 × 60?)	105–130 × 40–72	400 × 100	119 × 61	92–98 × 53–60
Receptaculum seminis (length × diameter in μ)	—	96 × 46	250–275 × 140–155	196–210 × 75–108	189 × 146	150 × 70	120–150 × 120–150	enlarged	large	60–90 × 40–50
Host	*Totanus calidris*	*Totanus stagnalis*	*Tringa glareola*	*Tringa stagnatilis*	*Tringa hypoleucos*	*Actitis macularia*	*Actitis macularia*	*Butastur indicus*	*Tringa glareola*	*Tringa glareola*

small scolex, small cirrus-sac, but many testes. The two species described by Burt (1940) are well separated on the constant difference in number of testes and in view of the fact that the cirrus-sac in *glareolae* appears to be significantly larger than that in *stagnatilidis*, even though the outside lower limit of the former overlaps with the upper limit of the latter. Singh (1952), describes the scolex of *hypoleuca* as 0·634–0·672 mm. × 0·48–0·63 mm. These measurements, however, are at variance with the figure he draws and the difference does not seem to be merely a matter of a factor of 10. The suckers are described as 0·043–0·052 mm. in diameter, while the diameter of the scolex is, as stated above, 0·48–0·63 mm. In his drawing, Singh figures four suckers on the scolex and the sizes of the suckers drawn are such that it would be possible to place three suckers, side by side, and still not project beyond the side of the scolex. Thus, the scolex diameter must be about 130 μ or 0·130 mm. According to the scale given, the breadth of the scolex across the suckers is about 110 μ. Thus, it seems unlikely that the measurements given by Singh refer to the scolex of this species at all and should probably be completely ignored. However, the large size of the cirrus-sac and the large number of testes all serve to separate it from any of the other species. *K. bodkini* resembles both *glareolae* and *stagnatilidis* in many respects, but can be separated from both species on account of the size of the cirrus-sac. In *bodkini*, even the largest cirrus-sac present, which was measured personally from the holotype and paratype material, is still 40 μ smaller than the lower limit quoted by Burt (1940) for *stagnatilidis*. Finally, the small number of testes in *susanae* n. sp. serves to separate it from any of the other species. The small cirrus-sac also separates it from *glareolae*, *stagnatilidis* and *hypoleuca*.

The new species described above has been named *susanae* in grateful recognition of the help received from Miss Susan Burt in the preparation of this manuscript.

Genus ***ASCOMETRA*** Cholodkovsky, 1913

Ascometra (?) sp.

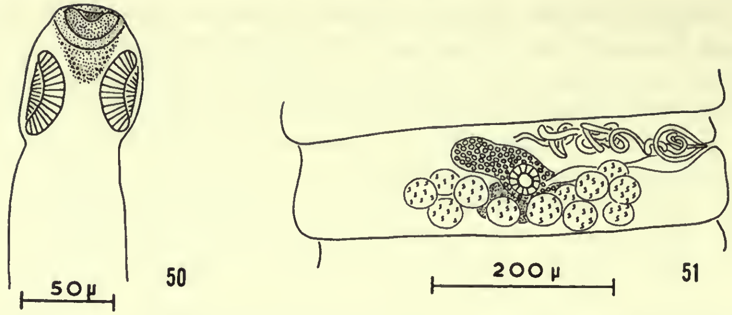
(Text-figs. 50–52)

HOST. *Centropus toulou* 8927.

The strobila measures 55 mm. long by 0·9 mm. in maximum breadth. The immature and mature proglottides are up to three times as broad as they are long, while the length of the gravid proglottides is up to twice the breadth. The genital apertures are almost unilateral, only 5% of the apertures occurring on the other side. The apertures in this 5% all occur singly.

The scolex (Text-fig. 50) is 82 μ long and 62 μ in diameter. There may be four suckers present, but the only two seen clearly are 45–50 μ in long diameter. Sucker spines are not present. For a description of the rostellum (?) see the discussion following this description.

There are 6–13 testes (Text-fig. 51) lying mainly posteriorly to the ovary although they may come to lie laterally in some proglottides. The testes measure 37–52 μ × 30–40 μ. The cirrus-sac, 52–64 μ long by 30–50 μ in diameter, is situated laterally about one-third the length of the proglottis from the anterior margin. The cirrus,



FIGS. 50 and 51. *Ascometra* (?) sp. Scolex (Fig. 50) and mature proglottis (Fig. 51)

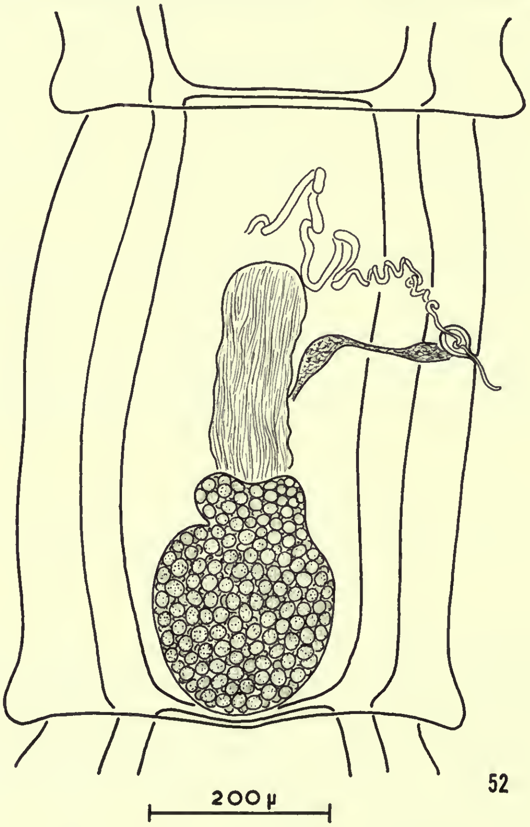


FIG. 52. *Ascometra* (?) sp. Gravid proglottis.

apparently unarmed and short, could be seen in a few proglottides projecting from the cirrus-sac. The largest cirrus seen was 35 μ long by 4 μ in diameter.

The bilobed ovary tends to be slightly displaced towards the aporal side of the proglottis but as it is not lying flat in the majority of proglottides, its full extent is difficult to determine accurately. Immediately behind the isthmus of the ovary is the ovoid vitelline gland which measures 50–75 μ × 45–60 μ. The vagina, which opens into the genital atrium posteriorly to the opening of the cirrus-sac, is relatively short, opening into a small receptaculum seminis which lies almost immediately behind the cirrus-sac. The receptaculum seminis measures 35 μ × 20 μ.

The uterus (Text-fig. 52) exists as a simple sac-like structure initially which lies in the posterior half of the proglottis within the medulla and not extending beyond the the excretory vessels. Just in front of the uterus lies the paruterine organ which gradually surrounds the uterus and rounds it off into an almost spherical structure.

Discussion. The structure of the scolex is very difficult to ascertain as it is lying in such a position that what at first sight looks like a rostellum may in fact be a third sucker superimposed on a fourth one. In the event that the scolex bears four suckers and no rostellum, it is almost certain that the worm belongs to the genus *Ascometra* Cholodkovsky, 1913, or perhaps to the genus *Orthoskrjabinia* Spassky, 1947. If the genital apertures are considered as being unilateral, thereby ignoring the 5% of genital apertures which appear on the " wrong " side, the worm should belong to the genus *Ascometra*; but if, on the other hand, the genital apertures are simply considered as irregularly alternating, this character would place the worm in Spassky's genus *Orthoskrjabinia*. In view of the fact that in neither of the two mentioned genera does there exist a worm which agrees sufficiently well with the present worm to warrant identification with it, and in view of the fact that the worms are ton in good enough state of preservation to allow a full description, it has been thought best that the present material be left unidentified until such a time as more material from *Centropus toulou* becomes available.

Genus ***NOTOPENTORCHIS*** Burt, 1938

Notopentorchis collocaliae Burt, 1938

(Text-figs. 53–55)

Host. *Apus affinis* 8784.

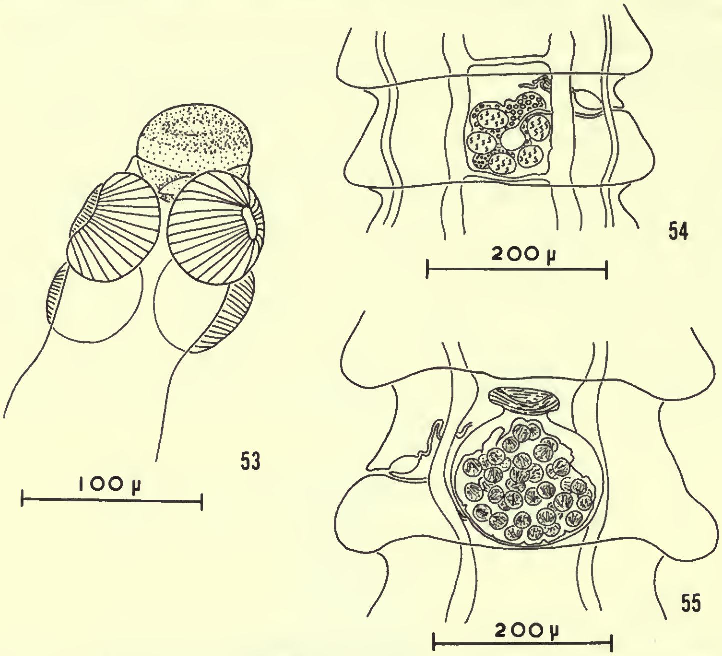
The worm is 20 mm. long and 0·48 mm. in maximum breadth. The proglottides are all, except for some of the most gravid ones, broader than long, the ratio of breadth to length varying from 4 : 1 to 3 : 2. The genital apertures are irregularly alternating and the genital ducts pass ventrally to the excretory vessels.

The scolex (Text-fig. 53) measures 110 μ in diameter and has a length, including the length of the rostellum, of 120 μ. The suckers are 65–70 μ × 50–55 μ and are unarmed. The rostellum, 60 μ long by 70 μ in diameter, is also unarmed but it is presumed that the hooks of the rostellum have been lost.

There are usually five testes (Text-fig. 54), but an occasional proglottis may contain four or six testes. These are situated posteriorly and laterally to the female genitalia with a tendency also to overlie parts of the ovary and the vitelline gland and they measure 25–30 μ × 18–22 μ. The cirrus-sac is small and most easily seen in gravid proglottides where it measures 30–35 μ in length by 16–20 μ in diameter.

The ovary, lying in the centre of the proglottis, is large and irregularly lobular, while the vitelline gland, which lies posteriorly to the ovary, is also well developed and measures 40–45 μ in diameter. Situated above the posterior part of the ovary is the shell-gland which has a diameter of 30–35 μ. The vagina, which opens into the genital atrium posteriorly to the opening of the cirrus sac, passes ventrally to the excretory vessels and opens into a receptaculum seminis which, in gravid proglottides where it reaches its maximum size, measures 24–33 μ × 16–20 μ.

The uterus is initially present as a simple sac which rounds off to form a sphere, 120–180 μ in diameter (Text-fig. 55). There are 20–35 eggs per proglottis and the contained oncospheres measure 30–38 μ × 24–30 μ. The hooks of the oncosphere are of two different sizes: the two lateral pairs are smaller, measuring 13–15 μ in length while the medial pair is larger, measuring 16–20 μ in length.



Figs. 53–55. *Notopentorchis collocaliae* Burt, 1938. Scolex (Fig. 53), mature proglottis (Fig. 54), and gravid proglottis (Fig. 55).

Discussion. The present material agrees very closely with the Ceylon material described by Burt (1938*a*) as *Notopentorchis collocaliae* for which he created a new species and erected a new genus. Baer (1959), however, transfers to the genus *Notopentorchis* Burt, *Paruterina javanica* Hübscher, 1937 and *P. bovieni* Hübscher, 1937 and places *N. collocaliae* as a synonym of what is now *Notopentorchis javanica* (Hübscher, 1937). In Burt's paper, the number of rostellar hooks is not given and Baer estimates the number, from the drawing of the scolex, to be about 50. Through the kindness of Mr. D. R. R. Burt, I have been able to examine the type material of *Notopentorchis collocaliae* and find there to be between 30–35 hooks, probably about 32. As there are at least 50 hooks in *javanica*, according to Baer who re-examined the type material of Hübscher, this would seem to represent a valid differentiating character. This difference, taken with the significant difference in the size of the cirrus-sac, undoubtedly separates these two worms and, accordingly, it is proposed here that *Notopentorchis collocaliae* is a valid species and should not be regarded as a synonym of *N. javanica*. Singh (1952) describes the species *Notopentorchis micropus* from *Micropus affinis*. Although his species differs from *collocaliae* " in the shape of the hooks, the size of the hooks of the two crowns, size of cirrus pouch, shape of ovary and development of uterus and paruterine organ ", it does not differ from Hübscher's species, *javanica*, with which Singh did not compare it. The apparent difference in number of testes (5 in *micropus* and 8–10 in *javanica*) is not a valid difference as re-examination of Hübscher's type material of *javanica* by Baer indicated that there were never 8–10 testes but only 5. Mokhehle (1951) creates the species *Sphaeruterina caffrapi* which appears to differ from *Notopentorchis javanica* only in the fact that the genital ducts pass dorsally to the excretory vessels instead of ventrally. Baer (1959), however, points out that while the genital ducts are described as passing dorsally to the excretory vessels, they are drawn as passing ventrally. Mokhehle (1951) described a second species of *Sphaeruterina*, namely *S. dikeniensis*, and again describes the genital ducts as passing dorsally to the excretory vessels but draws them as passing ventrally. Baer assumes that Mokhehle is correct in his drawing but wrong in his description and believes that both worms should be in the genus *Notopentorchis*, the first one as a synonym of *javanica* and the second, *Sphaeruterina dikeniensis*, as a synonym of *Notopentorchis vesiculigera* (Krabbe, 1882). The accompanying table (Table XII) best illustrates the differences between the four valid species of *Notopentorchis*.

TABLE XII

Valid species of *Notopentorchis* compared with material from Borneo.

Species:	*vesiculigera* Krabbe, 1882	*bovieni* Hübscher, 1937	*javanica* Hübscher, 1937		*collocaliae* Burt, 1938	Borneo material
Descriptions taken from:	Krabbe (1882)	Hübscher (1937)	Hübscher (1937)	Baer (1959)	Burt (1938*a*)	
Strobila (length × max. breadth in mm.)	100 × 1·5	78 × 0·918	26·5 × 0·5	25 × 0·59	26 × 0·29	20 × 0·48
Scolex (diameter in μ)	—	408	228	183–260	150	110
Rostellum (diameter in μ)	—	252	135	90–100	82	70
Rostellar hooks (number)	50	70	44–48	50	30–35 (personal count from type material)	hooks lost
Rostellar hooks (length in μ)	37–46 & 20–26	60 & 30	25–28	30–31 & 25–26	27 & 24	
Suckers (diameter in μ)	—	180–228	102	68–75 × 57–75	75	65–70 × 50–55
Testes (number)	—	9–12	8–10	5–6	5	5 (4–6)
Cirrus sac (length × diameter in μ)	—	150–170 × 40	110–120 × 40–50	57–68 × 23	35 × 30	30–35 × 16–20
Oncospheres (diameter in μ)	—	39 × 24	27–30	31–32	28	30–38 × 24–30
Oncosphere hooks (length in μ)	17–19	18	15	—	19	13–15 × 16–20
Host	*Hirundo rustica* *Cypselus apus*	*Macropteryx longipennis*	*Macropteryx longipennis*	*Apus caffer*	*Collocalia unicolor*	*Apus affinis*

Family **ACOLEIDAE** Fuhrmann, 1907

Genus ***GYROCOELIA*** Fuhrmann, 1899

Gyrocoelia perversa Fuhrmann, 1899

(Text-figs. 56–59)

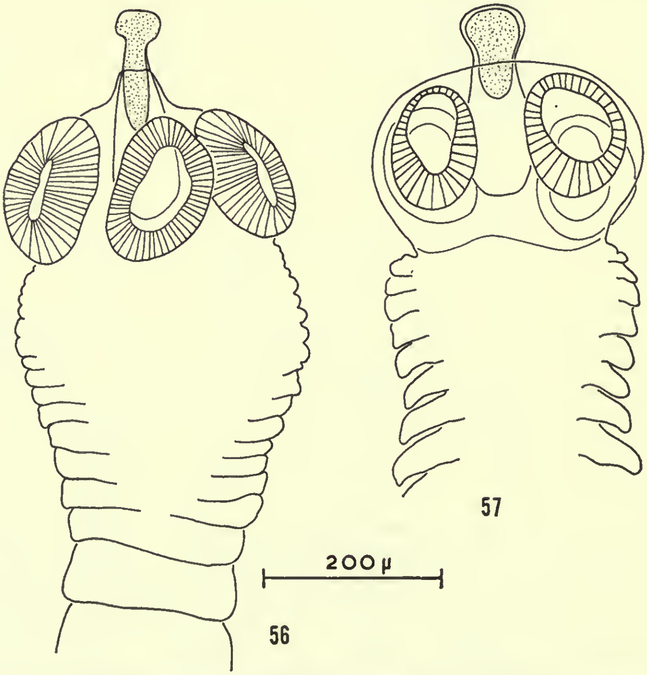
Gyrocoelia paradoxa (von Linstow, 1906) Fuhrmann, 1908.
Gyrocoelia milligani Linton, 1927.
Gyrocoelia pagollae Cable and Myers, 1956.

HOST. *Charadrius leschenaultii* 8999; 9334.

One full mature " female " strobila was found in host 8999, and two small, barely mature worms—one male and one " female "—were found in host 9334.

The scolex (Text-figs. 56 and 57) measures 290–325 μ in diameter by 250–280 μ in length including the length of the rostellum. The suckers are oval in outline and measure 145–170 μ × 100–125 μ. No sucker spines were seen. The rostellum measures 150–250 μ from the top of the apical cushion to the bottom of the rostellar sac and the diameter of the apical cushion is 50–80 μ. No rostellar hooks were seen.

The male strobila (Text-fig. 58) is not fully mature although, in the distal part of the strobila, several cirri can be seen in various stages of extrusion. The length of the strobila is 8 mm. and the maximum breadth is 0·9 mm. The testes are present in a compact group about the centre of the proglottis, but are so crowded together that it is not possible to make an accurate count of their number. There appear to be,

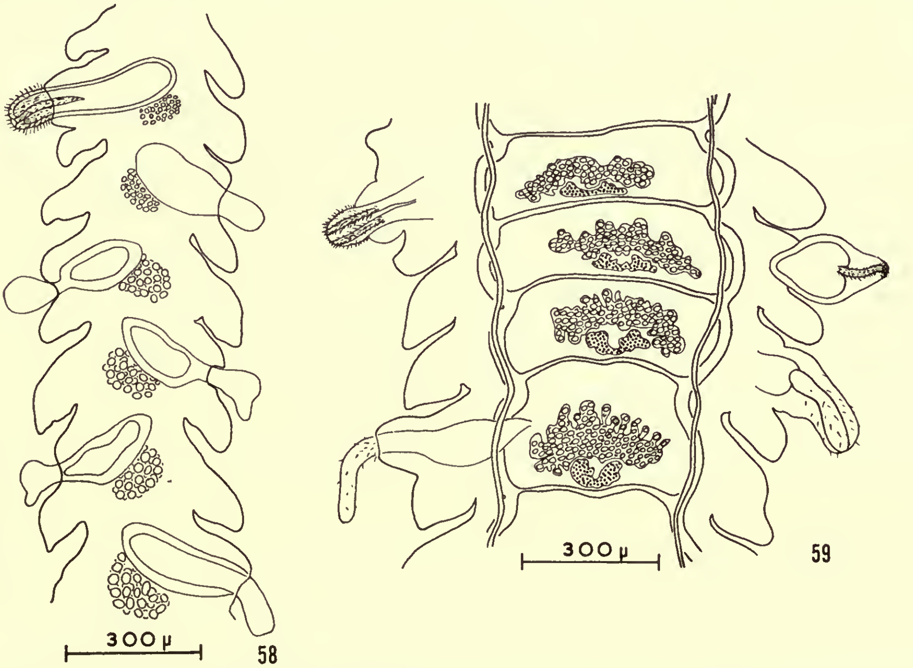


FIGS. 56 and 57. *Gyrocoelia perversa* Fuhrmann, 1899. Scolex with everted rostellum (Fig. 56) and scolex with retracted rostellum (Fig. 57).

however, about 30 testes, the maximum diameter of the most mature testes present being 30–40 μ. The cirrus-sac measures 240–280 μ × 120–130 μ and passes between the ventral and the dorsal excretory canals. The conical cirrus measures about 250 μ in its extended form, has a diameter of 75 μ at its base, and a diameter of about 35 μ at its apex. During the early part of its extrusion, the long spines present on the proximal quarter of the cirrus are easily seen and these measure 10–15 μ in length when measured from a whole mount.

The smaller " female " strobila is very similar in external dimensions to the small male, while the larger " female " (Text-fig. 59) measures 53 mm. long by 2·5 mm. in maximum breadth. The ovary is a little over 500 μ across by 50–100 μ. The elongated vitelline gland measures 230–250 μ × 30–45 μ. The " receptaculum seminis " could be seen lying between the ovary and the vitelline gland. In the larger of the two worms, the cirrus-sac measures 420–500 μ × 110–150 μ; while in the smaller worm the cirrus-sac is 300–320 μ × 120–140 μ. The eggs, present only in the larger worm, measure 68–73 μ × 35–40 μ while the contained oncospheres are 20–30 μ in diameter. The hooks of the oncosphere were not examined as squash preparations, but on a whole mount these appeared to be about 8 μ long.

The muscular system is very well developed and comprises 100–150 large bundles of longitudinal muscle fibres in two poorly separated layers. Each bundle contains up to 100 individual muscle fibres. The transverse muscles lie between the longitudinal muscle bundles and also round the central medulla. Close to the cuticle lie further individual longitudinal muscle fibres interspersed with large parenchyma cells.



FIGS. 58 and 59. *Gyrocoelia perversa* Fuhrmann, 1899. Part of a male strobila (Fig. 58) and part of a " female " strobila (Fig. 59).

Discussion. The present material agrees reasonably closely with that described by Baer (1959) as *Gyrocoelia perverse* Fuhrmann, 1899(*b*). Baer places all known species of *Gyrocoelia* plus *Infula burhini* Burt, 1939(*b*), into two groups. The first of these groups contains *Gyrocoelia australiensis* Johnston, 1912; *G. fausti* Tseng-Shen, 1933; *G. kiewietti* Ortlepp, 1937; *Infula burhini* Burt, 1939; and *Gyrocoelia albaredai* López-Neyra, 1952, all of which become synonymous with *Gyrocoelia crassa* (Fuhrmann, 1900) Baer, 1940. The second group contains *Gyrocoelia paradoxa* (von Linstow, 1906) Fuhrmann, 1908; *G. milligani* Linton, 1927 (see also Webster, 1943*b*); and G. *pagollae* Cable and Myers, 1956, all of which become synonymous with *Gyrocoelia perversa* Fuhrmann, 1899.

Although at first sight there appear to be several differences between the two groups, few of these are significant. Perhaps the most striking differences are found in the size of cirrus-sac, the number of testes and the diameter of the scolex. In *perversa*, the cirrus-sac tends to be smaller and measures up to about 400 μ × 137–146 μ, while in *crassa*, the length of the cirrus-sac reaches up to 650 μ and its diameter is 195–260 μ. In *perversa* there tend to be fewer testes, numbering 20–30, whereas in *crassa* the number ranges from 30 to 50 per segment. Although the upper number of testes in *perversa* coincides with the lower number of testes in *crassa*, the average number of testes found in any one worm can usually place it unambiguously into one or other of the two species. Finally, in *perversa* the diameter of the scolex is about 320 μ whereas in *crassa* it is considerably greater, measuring 411–457 μ. It is not unlikely that there exists a graded series of forms and that one worm may exhibit features in common with both species. For instance, the present material possesses about 30 testes and thereby lies about half-way between *perversa* and *crassa*. Another feature which would place it in this anomalous position is the size of the cirrus-sac, particularly that of the large " female " strobila which, although far from reaching the upper limit of size of cirrus-sac found in *crassa*, is nevertheless substantially bigger than the cirrus-sac described for *perversa*. The size of the scolex, the diameters of the suckers, and, to a certain extent, the overall size of the worm all indicate that it is *perversa*.

Owing to the fact that the present material possesses no rostellar hooks, it was first thought that the worms belonged to the genus *Infula* Burt, 1939. The two main features of difference between *Infula* and *Gyrocoelia* are that *Infula* is dioecious and there are no rostellar hooks whereas in *Gyrocoelia* there are rostellar hooks, and initially the worm was considered by most as a normal hermaphrodite worm. Early workers described *Gyrocoelia* as possessing testes and ovaries in the same strobila and, furthermore, in some cases actually figured them together in the same proglottis. However, Baer (1959), by re-examining much of the type-material, has been able to show that testes do not occur in the same strobilae as ovaries. Furthermore, Baer examined the type-material of *Infula burhini* Burt, 1939, but was unable to substantiate Burt's hypothesis that the structure corresponding to the cirrus-sac in the male, functioned as a vagina in the female, particularly as he could not find sperm in the proximal portion of the " vagina " where it should undoubtedly be in the event of that structure functioning as a vagina. In view of this, and in view of the fact that it is generally recognized that the rostellar hooks of *Gyrocoelia* are highly caducous, Baer felt justified in treating *Infula* as a synonym of *Gyrocoelia* and making *Infula burhini* a synonym of *Gyrocoelia crassa*. The fact that sperm are found in the " receptaculum seminis " is explained by Baer with the hypothesis that the female strobilae are cryptohermaphrodite and that sperm are produced by testicular tissue which is present in the walls of the " receptaculum seminis ".

Although Baer considers that *Infula* should belong to the genus *Gyrocoelia*, on the grounds stated, it is by no means improbable that *Infula* may well be a valid genus, principally on the basis of its lacking rostellar hooks. Recognizing that rostellar hooks may easily be lost in fixing and preserving worms, towards the end of his discussion on *Infula burhini*, Burt (1939*b*) states the following:

" The worms described in this paper were obtained in the field from birds shot for their parasites. They were fixed in Bouin's fluid on the spot, hence their state of preservation and fixation is good. Cestodes collected under these conditions and before fixation allowed to detach themselves from the wall of the gut by placing the opened gut in water, very rarely lose their rostellar hooks. Thus one has little hesitation in accepting the absence of hooks in the six specimens as being a diagnostic character. *Infula* is most nearly allied to *Shipleya* and *Gyrocoelia*, and is distinguished from these, apart from its dioecious character, by the character of the rostellum. The rostellum is absent in *Shipleya*, a fact which was ascertained by Fuhrmann from sections of the scolex; it is present and characteristically armed in *Gyrocoelia*; and present but unarmed in *Infula*."

Coil (1955*b*) describes a new species of *Infula*, namely *I. macrophallus*, and in a later paper (Coil, 1963) he discusses the validity of the genera *Gyrocoelia* and *Infula*. His conclusions, which are based on careful examination of worms from freshly killed hosts, indicate that not only is the scolex of *Infula* consistently unarmed, but that there are highly significant differences in the egg membranes of members of the two genera. These differences are elegantly shown by using various histochemical techniques such as those used by Ogren (1958, 1959*a* and *b*, and 1961).

Burt has recently made a large collection of worms from wading birds in North America and it is hoped that examination of this new, carefully fixed and preserved material, will throw further light on the genus *Infula* particularly in relation to the cryptotestes suggested by Baer.

From the same host species, namely *Charadrius leschenaultii*, there were found what appear to be three different worms all of which, however, almost certainly belong to one or other of the families Acoleidae, Progynotaeniidae, and Dioecocestidae. Brief descriptions of them are given here due to their probable relationship with *Gyrocoelia* and they are described simply under the headings of Species 1, Species 2 and Species 3.

Species 1.

This is represented by three small worms in poor state of preservation which probably belong to the genus *Progynotaenia*, or perhaps *Andrepigynotaenia*. The longest worm measues 6 mm. long by 0·7 mm. in maximum breadth. The genital apertures are irregularly alternating.

The scolex has a diameter of 150 μ and is 150 μ long, the length being taken to include the length of the rostellar sac. The four suckers are approximately 75 μ in diameter but appear to be degenerating. No sucker spines were seen. The rostellum measures about 60 μ long, the rostellar sac about 90 μ long, and the apical cushion has a diameter of 52 μ. No rostellar hooks were seen, but there appear to be 11 or 12 scars present on the rostellum which may well mark the sites of hooks that have been lost.

Although the worm is not in a very good state of preservation there appear to be about 7 testes, the range possibly being 6–10, which have a diameter of 30–40 μ. These were best seen lying alongside the developing uterus and were scarcely visible in any but two proglottides. The cirrus-sac is 150–200 μ long by 70–80 μ and is not fully developed until the uterus is well formed and the ovary and vitelline gland have both disintegrated. There does not appear to be either an external nor an internal seminal vesicle, the vas deferens lying slightly twisted and swollen outside the cirrus-sac and the ductus ejaculatorius lying in a few loops in the proximal portion of the cirrus-sac.

The ovary measures about 125 μ × 90 μ just before it starts to enlarge with what appear to be fertilized eggs. The vitelline gland, situated ventrally and posteriorly to the ovary, is more or less spherical with a diameter of about 70 μ. The receptaculum seminis is large, measuring up to 230 μ × 110 μ, and can be seen in several proglottides as a swollen sac full of sperm.

There are no fully-gravid proglottides but in the more mature proglottides, the uterus can be seen as a large sac-like structure almost completely filling the medulla of the proglottis.

Species 2.

This is represented by one worm, 9 mm. long and 0·52 mm. in maximum breadth. The proglottides tend to be triangular in shape, longer than broad initially but becoming slightly broader than long. The genital apertures are regularly alternating.

The scolex has a diameter of 175 μ across the suckers and a length of 180 μ including the length of the rostellum. The four suckers are 85–95 μ in diameter and appear to be unarmed. The rostellum also apparently unarmed, measures 144 μ from its tip to the bottom of the rostellar sac.

The strobila appears to comprise solely male proglottides, but owing, perhaps, to the poor state of preservation, no testes were seen. The cirrus-sac is large and in many of the more distal proglottides, could be seen projecting well beyond the lateral margin of the strobila. It measures 315–350 μ long by 110–130 μ in diameter and in early proglottides can be seen to contain a large, profusely spined, cirrus. In the later proglottides, when the cirrus, which reaches over 300 μ in length, has been extruded, the spines are no longer visible and presumably have been lost.

No other anatomical features could be made out.

Species 3. (Text-fig. 60).

This species is represented by a single worm with a scolex which bore three hooks. The material is in an advanced state of decomposition and the only data of any significance is the shape and size of the hooks.

Measured under oil immersion in a squash preparation, the hooks (Text-fig 60) are 85 μ, 86 μ and 89μ long, although one, the largest, is slightly twisted.

Discussion. Although Webster (1951) gives a useful table of species in the genera *Progynotaenia* and *Proterogynotaenia* and Sandeman (1959*b*) gives a more recent review of the genus *Proterogynotaenia*, none of the above three species could be identified. There is only one worm described in the genus *Andrepigynotaenia* Davies and Rees, 1947, and that has many more testes (58–70) than is apparent in any of the above. It may be that one or more of the above three represents a new species but, as the material is neither in good condition nor complete, the erection of any new species is hardly justified.

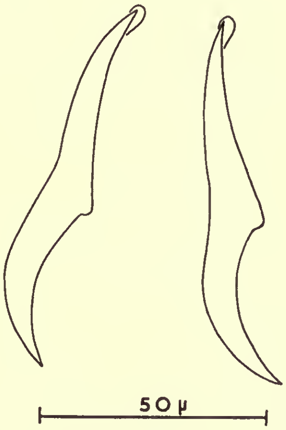


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Fig. 60. Species 3. Rostellar hooks.

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By M. H. THURSTON & ELIZABETH ALLEN

INTRODUCTION

The collections of the Crustacea Malacostraca in the British Museum are now being thoroughly catalogued for the first time since Adam White produced his list in 1847. This complete documentation will eventually provide easier and more rapid access to the data concerning all the specimens in the collection but will take several years to achieve. In the meantime it is felt that as convenient sections of the work are completed the publication of lists of the holdings of type material will be of service to taxonomists. This first list thus consists of the types of the first four amphipod families to be catalogued.

HISTORICAL

Crustacea were poorly represented in the Museum of Sir Hans Sloan, which, in 1753, formed the nucleus of the British Museum collections. It is probable that prior to the acquisition of the Leach Collection in 1826 the Amphipoda were unrepresented in Museum collections. White (1847) listed a total of about 260 amphipod specimens belonging to 69 species. The great majority of these specimens were dry-mounted on pins in insect cabinets. In 1856 Bate was commissioned to catalogue the amphipod collection. The resultant catalogue (Bate, 1862) listed all species described up to that time and indicated that a total of 209 species were represented in the Museum collections.

During the latter half of the nineteenth century, the amphipod collection was considerably increased as a result of scientific expeditions and private collections donated by members of the armed forces, colonial administrators and private individuals. This trend has continued, with minor checks, until the present day.

Much information concerning the early history of the Museum collections can be found in Bell (1906) and Günther (1912).

Some of the more important accessions to the amphipod collection are listed below.

68 : 107	Presented by William Stimpson at some time prior to 1862 and containing type material of about 15 species.
76 : 5	75 Lake Baikal species purchased from Prof. Taczanowski.
80 : 21	66 species from the British Isles presented by Rev. T. R. R. Stebbing.
85 : 22	22 Australian species presented by the Australian Museum. This material appears to have been identified by Haswell and contains type material of about 10 species.

1889 : 5 : 15	About 2000 specimens collected by H.M.S. "Challenger", identified by Stebbing (1888) and presented by the Lords of the Treasury. About 260 species were represented, of which 169 were new.
1902 : 11 : 5 1903 : 10 : 5	Material collected by "Southern Cross" Expedition (1898–1900) in the Antarctic. Determined by A. O. Walker (1903) and presented by Sir George Newnes. 20 species represented, of which 14 were new.
1905 : 2 : 18	Amphipoda collected by the staff of the Ceylon Pearl Fisheries Investigations and presented by Prof. W. A. Herdman. Walker (1904) identified 67 species, of which 36 were new.
1907 : 6 : 6 1907 : 6 : 13	National Antarctic Expedition (1901–04) aboard the "Discovery". Walker (1907) determined 54 species, 19 of them new.
1909 : 1 : 29 1909 : 2 : 1 1909 : 2 : 13 1909 : 2 : 15	Material from various sources in the Indian Ocean worked up by Walker (1909). Seven new species in a total of 82.
1911 : 11 : 8	Amphipods from the Norman Collection. 1896 lots of specimens representing 702 species and including type material of 101 species. The total number of specimens registered is 11460, but the actual total is about 20000. Canon A. M. Norman corresponded with all the leading carcinologists of his day, and during the period 1865–1911 acquired many specimens from them and from most of the Museums and Institutions throughout Europe. He was was also an untiring collector himself, visiting many localities in the British Isles and Scandinavia. The collection contains material from the Arctic, from Europe, Scandinavia, the Mediterranean Sea, the eastern seaboard of America, and the temperate North Atlantic.
1925 : 9 : 8	The Walker Collection containing 447 lots of material of 197 species and including type material of at least 20 species. The number of specimens registered is 2012 but the actual number is about 3500. The bulk of this material is either from collections which passed through Walker's hands, or which he himself collected in North Wales and Brittany.
1928 : 4 : 2	A total of 75 South African species, including syntypical material of 41 species, presented by Dr. K. H. Barnard.
1928 : 12 : 1	The Stebbing Collection comprising 321 species and including type material of 18 species. The total number of specimens registered is 1383, but the collection probably contains about 2000 specimens in all.

1930 : 8 : 1	A collection obtained by the British Antarctic ("Terra Nova") Expedition, 1910–13. Barnard (1930) described 35 new species and identified a further 119 species.
1934 : 5 : 8	Material collected by the Great Barrier Reef Expedition, identified by Barnard (1931*a*) and containing 38 species of which 3 were new.
1936 : 3 : 18	Material obtained by exchange with the Zoological Institute of the Soviet Academy of Sciences, Leningrad. 92 species from Russian Seas.
1936 : 11 : 2	Specimens collected during the first two years of operations conducted by the "Discovery" Committee in Antarctic waters. The collection worked up by Barnard (1932) contains 323 species of which 97 are represented by type material.
1938 : 1 : 3	The "John Murray" Collection obtained from the Red Sea and NW Indian Ocean was worked up by Barnard (1937) and contained 116 species of which 8 were new.
1947 : 11 : 4	38 species including 2 types series, presented by Mrs. Tattersall, mostly from deep water off the W coast of Ireland.
1952 : 5 : 7	Material from the Spence Bate Collection which remained unincorporated until 1952. 104 species are present, of which 44 are represented by type material.
1961 : 8 : 1	Specimens collected by the "Atlantide" Expedition to W Africa (Reid, 1951). 12 of the 92 species present in the Museum were new.
1965 : 2 : 4 1965 : 2 : 9	186 lots of freshwater amphipods from the British Isles, presented by H. B. N. Hynes.
1967 : 1 : 12	42 species of Lake Baikal amphipods presented by Prof. Dr. E. Gurjanova of the Zoological Institute of the Soviet Academy of Sciences, Leningrad.
1967 : 6 : 2	700 specimens in 58 lots representing 37 species collected at Plymouth by one of us (M.H.T.).

The nomenclature used is that given by Barnard (1958). Subsequent revisions, some quite radical, have been ignored. This is due not to any doubt as to their validity, but because it was felt that a readily accessible list of names under one cover would reduce confusion and ambiguity to a minimum.

Valid species have been listed under the name appearing in Barnard (1958), and followed by the author, date and page of publication. The name under which the species was first described is included in square brackets if it differs from the current name. In the case of species which have been submerged, the original name, in square brackets, is followed by the name of the taxon currently held to include that species, and the authority for the transference. Species described since the compilation of Barnard (1958) are recorded under their original name.

SYNOPSIS OF SPECIES REPRESENTED IN BRITISH MUSEUM (NATURAL HISTORY) COLLECTIONS*

	Lysianassidae		Stegocephalidae		Ampeliscidae		Haustoriidae	
	Barnard (1958)	B.M. (N.H.)	Barnard (1958)	B.M. (N.H.)	Barnard (1958)	B.M. (N.H.)	Barnard (1958)	B.M. (N.H.)
No. of genera	101	66	17	12	5	4	13	8
No. of valid species	395	186	34	20	121	52	54	21
No. of dubious species	26	9	2	0	3	2	2	2
Types of valid species	—	97	—	11	—	27	—	13
Types of dubious species	—	5	—	0	—	2	—	1
Types of transferred species	—	15	—	1	—	3	—	3

* Categories as in Barnard, 1958.

The type-status of the specimen or specimens is given together with the registration number, locality data, number of specimens and the means of preservation (i.e. alcohol, microslides, or dry). There is doubt over the exact status of some of the type material from the Norman Collection. Norman marked as " cotype " specimens of any species which he received from the author of the species concerned. It has not been possible, in a few cases, to relate exactly the locality on the label with that given in the original description. Where there is doubt, this is indicated in the text. Localities of " Discovery " material determined by K. H. Barnard and marked thus * are those nominated as " Types " in his report (Barnard, 1932).

This list includes type material incorporated into the collections up to and including 31 March 1968.

The authors acknowledge with thanks the help and encouragement given them by Dr. A. L. Rice and Mr. R. W. Ingle.

Family **LYSIANASSIDAE**

ACIDOSTOMA Liljeborg

Acidostoma obesum (Bate) 1862 : 74 [*Anonyx obesus*].

HOLOTYPE: Reg. no. 1952 : 5 : 7 : 2 (alcohol).
LOCALITY: Moray Firth, Scotland.
COLLECTION: Bate.

ACONTIOSTOMA Stebbing

[*Acontiostoma magellanicum*] Stebbing 1888 : 714 (transferred to *Acontiostoma marionis* Stebbing by Barnard 1932).

HOLOTYPE: Reg. no. 1889 : 5 : 15 : 34 (4 slides).
LOCALITY: Sta. 313. Off Cape Virgins, Patagonia, 52° 20′ S 67° 39′ W, 55 fm, 20 January 1876.
COLLECTION: " Challenger ".

Acontiostoma marionis Stebbing 1888 : 709.

HOLOTYPE: Reg. no. 1889 : 5 : 15 : 33 (specimen in alcohol + 6 slides).
LOCALITY: Sta. 145. Off Marion Island, South Indian Ocean, 50–75 fm, 27 December 1873.
COLLECTION: " Challenger ".

ALLOGAUSSIA Schellenberg

Allogaussia lobata Barnard 1932 : 67.

SYNTYPE: Reg. no. 1936 : 11 : 2 : 346* (1 specimen, alcohol).
LOCALITY: Sta. 170. Off Cape Bowles, Clarence Island, South Shetland Islands, 61° 25′ S 53° 46′ W, 342 m, 23 February 1927.

SYNTYPES: Reg. no. 1936 : 11 : 2 : 347–348 (1 + 2 specimens, alcohol).

LOCALITY: Sta. 142. East Cumberland Bay, South Georgia, 88–273 m, 30 December 1926. Sta. 208. Off Livingston Island, South Shetland Islands, 800–(0) m, 7 April 1927.

COLLECTION: " Discovery " Committee.

Allogaussia navicula Barnard 1932 : 65.

SYNTYPES: Reg. no. 1936 : 11 : 2 : 340–345* (4 specimens, alcohol).

LOCALITY: Sta. 175. Bransfield Strait, South Shetland Islands, 63° 17′ S 59° 48′ W, 200 m, 2 March 1927.

SYNTYPES: Reg. no. 1936 : 11 : 2 : 337–339 (7 specimens, alcohol).

LOCALITY: Sta. 170. Off Cape Bowles, Clarence Island, South Shetland Islands, 61° 25′ S 53° 46′ W, 342 m, 23 February 1927.

COLLECTION: " Discovery " Committee.

AMARYLLIS Haswell

Amaryllis bathycephala Stebbing 1888 : 699.

HOLOTYPE: Reg. no. 1889 : 5 : 15 : 30 (specimen in alcohol + 4 slides).

LOCALITY: Sta. 161. Off Melbourne, Australia, 33 fm, 1 April 1874.

COLLECTION: " Challenger ".

Amaryllis tenuipes (Walker) 1904 : 241 [*Vijaya tenuipes*].

SYNTYPES: Reg. no. 1905 : 2 : 18 : 10 (1 specimen, alcohol).
1905 : 2 : 18 : 308–309 (2 slides).

LOCALITY: Ceylon, shallow water.

COLLECTION: Herdman.

AMBASIOPSIS Barnard

Ambasiopsis georgiensis Barnard 1931 : 425.

SYNTYPES: Reg. no. 1936 : 11 : 2 : 136–137 (3 specimens, alcohol).

LOCALITY: Sta. 159. 53° 52′ S 36° 08′ W, 320 m, 21 January 1927.

COLLECTION: " Discovery " Committee.

Ambasiopsis uncinata Barnard 1932 : 46.

SYNTYPES: Reg. no. 1936 : 11 : 2 : 146–148 (4 specimens, alcohol).

LOCALITY: Sta. 170. Off Cape Bowles, Clarence Island, South Shetland Islands, 61° 25′ S 53° 46′ W, 342 m, 23 February 1927.

COLLECTION: " Discovery " Committee.

ANONYX Krøyer

[*Anonyx ampulloides*] Bate 1862 : 78 (transferred to *Anonyx nugax* (Phipps) by Steele & Brunel, 1968).

HOLOTYPE: Reg. no. 68 : 107 (15) (alcohol).

LOCALITY: Japan.

COLLECTION: Stimpson.

Anonyx annulatus Bate 1862 : 79 (removed from *Anonyx* by Steele & Brunel, 1968, but correct generic position not indicated).

Holotype: Reg. no. 68 : 107 (13) (alcohol).
Locality: Japan.
Collection: Stimpson.

Anonyx bispinosus Steele 1967 : 257.

Holotype: Reg. no. 1966 : 3 : 28 : 1–2 (part) (1 specimen in alcohol + 12 slides).
Paratype: Reg. no. 1966 : 3 : 28 : 1–2 (part) (1 specimen, alcohol).
Locality: Off E coast of Kolguev Island, Barents Sea.
Collection: Stebbing.

Anonyx exiguus Stimpson 1853 : 51.

Syntype: Reg. no. 68 : 107 (29) (1 specimen, alcohol).
Locality: Off Cheney's Head, Grand Manan, Bay of Fundy, New Brunswick.
Collection: Stimpson.

Anonyx indicus Giles 1890 : 69.

Syntype: Reg. no. 1968 : 129 (1 slide).
Locality: Off the Seven Pagodas, Madras, India, 5–10 fm.
Collection: Giles.

[*Anonyx melanophthalmus*] Norman 1867 : 201 (transferred to *Orchomene hanseni* Meinert by Sars 1895).

Syntypes: Reg. no. 1911 : 11 : 8 : 13346 (1 specimen, alcohol).
1911 : 11 : 8 : M727–M729 (3 slides).
Locality: Sleat Sound, Isle of Skye, Scotland, 1866.
Collection: Norman.

Anonyx punctatus Bate 1862 : 78 (removed from *Anonyx* by Steele & Brunel, 1968, but correct generic position not indicated).

Holotype: Reg. no. 68 : 107 (14) (alcohol).
Locality: Behring Strait.
Collection: Stimpson.

ARISTIAS Boeck

Aristias antarcticus Walker 1906 : 454.

Syntypes: Reg. no. 1907 : 6 : 6 : 92–93 (2 specimens, alcohol).
Locality: McMurdo Sound, Ross Sea, 20 fm, 28 February 1902.

Syntypes: Reg. no. 1907 : 6 : 13 : 6–7 (2 slides).
Locality: no data, 5 June 1902.
Collection: National Antarctic Expedition.

Aristias collinus Barnard 1932 : 44.

Syntpye: Reg. no. 1936 : 11 : 2 : 134* (1 specimen, alcohol).

LOCALITY: Sta. 170. Off Cape Bowles, Clarence Island, South Shetland Islands, 61° 25′ S 53° 46′ W, 342 m, 23 February 1927.

SYNTYPE: Reg. no. 1936 : 11 : 2 : 135 (1 specimen, alcohol).
LOCALITY: Sta. 175. Bransfield Strait, South Shetland Islands, 63° 17′ S 59° 48′ W 200 m, 2 March 1927.
COLLECTION: " Discovery " Committee.

Aristias pacificus Schellenberg 1936 : 153.

SYNTYPES: Reg. no. 1967 : 1 : 10 : 17–42 (26 specimens, alcohol).
LOCALITY: NE corner of Union Bay, Vancouver, British Columbia, 16–20 fm, 4 July 1923 (In atrial cavity of *Ascidiopsis paratropa*).
COLLECTOR: Prof. C. H. O'Donoghue.

Aristias symbiotica Barnard 1916 : 121.

SYNTYPES: Reg. no. 1928 : 4 : 13 : 16–20 (6 specimens, alcohol).
LOCALITY: False Bay, South Africa. Cape Hangklip bearing NE ¼E, distance 27 miles, 105 fm, 26 February 1902. (From branchial cavity of Ascidians).
DONOR: South African Museum.

AROUI Chevreux

Aroui setosus Chevreux 1910 : 170.

SYNTYPES: Reg. no. 1912 : 4 : 4 : 5–7 (3 specimens, alcohol).
LOCALITY: NE of Cap de Garde, Golfe de Bône, Algeria, 65 m. On *Spatangus* sp.
COLLECTOR: E. Chevreux.

ARUGELLA Pirlot

Arugella falklandica (Barnard) 1932 : 39 [*Lysianassa falklandica*].

SYNTYPES: Reg. no. 1936 : 11 : 2 : 112* (1 specimen, alcohol).
LOCALITY: Sta. WS 85. 8 miles S66° E of Lively Island, East Falkland, Falkland Islands, 79 m, 25 March 1927.

SYNTYPES: Reg. no. 1936 : 11 : 2 : 113–114 (2 specimens, alcohol).
LOCALITY: Sta. WS 97. South Atlantic, 49°00′ S 61° 58′ W, 146–145 m, 18 April 1927.
COLLECTION: " Discovery " Committee.

[*AUSTRONISIMUS* Barnard]

[*Austronisimus rhinoceros*] Barnard 1931 : 425 (transferred to *Paralysianopsis odhneri* Schellenberg by Barnard 1932).

HOLOTYPE: Reg. no. 1936 : 11 : 2 : 108 (alcohol).
LOCALITY: Sta. WS 25. Undine Harbour, South Georgia, 18–27 m, 17 December 1926.
COLLECTION: " Discovery " Committee.

BATHYAMARYLLIS Pirlot

Bathyamaryllis haswelli (Stebbing) 1888 : 703 [*Amaryllis haswelli*].

HOLOTYPE: Reg. no. 1889 : 5 : 15 : 31 (specimen in alcohol + 8 slides).
LOCALITY: Sta. 78. Off the Azores, 37° 26′ N 25° 13′ W, 1000 fm, 10 July 1873.
COLLECTION: " Challenger ".

CHEIRIMEDON Stebbing

Cheirimedon crenatipalmatus Stebbing 1888 : 638.

HOLOTYPE: Reg. no. 1889 : 5 : 15 : 13 (4 slides).
LOCALITY: Sta. 149H. Off Cumberland Bay, Kerguelen, South Indian Ocean, 127 fm, 29 January 1874.
COLLECTION: " Challenger ".

Cheirimedon fougneri Walker 1903 : 41.

SYNTYPES: Reg. no. 1903 : 10 : 15 : 13–15 (9 specimens in alcohol + 11 slides).
LOCALITY: Ross Sea, 78° 35′S, surface, 18 February 1900.
COLLECTION: " Southern Cross ".

[*Cheirimedon hanseni*] Walker 1903 : 42 (transferred to *Cheirimedon crenatipalmatus* Stebbing by Schellenberg 1926).

SYNTYPES: Reg. no. 1903 : 10 : 5 : 20–22 (8 specimens in alcohol + 1 slide).
LOCALITY: Cape Adare, South Victoria Land, 7 fm, 1 November 1899.
COLLECTION: " Southern Cross ".

CHIRONESIMUS Sars

Chironesimus rotundatus (Barnard) 1925 : 329 [*Lakota rotundatus*].

SYNTYPES: Reg. no. 1928 : 4 : 13 : 28–35 (10 specimens, alcohol).
LOCALITY: South Africa.
DONOR: South African Museum.

CRYBELOCEPHALUS Tattersall

Crybelocephalus megalurus Tattersall 1906 : 33.

SYNTYPE: Reg. no. 1947 : 11 : 4 : 18 (1 specimen, alcohol).
LOCALITY: 50 miles N by W of Eagle Island, Co. Mayo, Eire, 1150 fm, May 1905.
COLLECTION: Tattersall.

CYCLOCARIS Stebbing

[*Cyclocaris faroensis*] Norman 1900 : 197 (transferred to *Cyclocaris guilelmi* Chevreux by Stebbing 1906).

SYNTYPE: Reg. no. 1911 : 11 : 8 : 12755 (1 specimen, alcohol).
1911 : 11 : 8 : M686 (1 slide).

LOCALITY: " Triton " Sta. 8. Faeroe Channel, 60° 18′ N 06° 15′ W, tow net at 640 fm, 1882.
COLLECTION: Norman.

Cyclocaris tahitensis Stebbing 1888 : 664.

HOLOTYPE: Reg. no. 1889 : 5 : 15 : 20 (3 slides).
LOCALITY: Off Tahiti, 2 October 1875. [This corresponds with Sta. 279. Off Papeete, Tahiti, 420–680 fm.]
COLLECTION: " Challenger ".

CYPHOCARIS Boeck

Cyphocaris challengeri Stebbing 1888 : 661.

HOLOTYPE: Reg. no. 1889 : 5 : 15 : 19 (4 slides).
LOCALITY: 400 miles N of the Sandwich Islands. [Probably near Sta. 256.]
COLLECTION: " Challenger ".

[*Cyphocaris micronyx*] Stebbing 1888 : 656 (transferred to *Cyphocaris anonyx* by Stebbing 1906).

SYNTYPE: Reg. no. 1889 : 5 : 15 : 17 (4 slides).
LOCALITY: Sta. 295. Off the West coast of South America, 38° 07′ S 94° 04′ W, 1500 fm, 5 November 1875.

SYNTYPE: Reg. no. 1889 : 5 : 15 : 18 (1 slide).
LOCALITY: Sta. 335. Near Tristan da Cunha, 32° 24′ S 13° 05′ W, 1425 fm, 6 March 1876.
COLLECTION: " Challenger ".

EUONYX Norman

Euonyx chelatus Norman 1867 : 202.

SYNTYPES: Reg. no. 1911 : 11 : 8 : 13684–13686 (3 specimens, alcohol)
1911 : 11 : 8 : M843–M845 (3 slides).
LOCALITY: Sleat Sound, Isle of Skye, Scotland, July 1866.
COLLECTION: Norman.

Euonyx normani Stebbing 1888 : 669.

HOLOTYPE: Reg. no. 1889 : 5 : 15 : 21 (specimen in alcohol + 8 slides).
LOCALITY: Sta. 170A. Near Kermadec Island, South Pacific, 29° 45′ S 178° 11′ W, 630 fm, 14 July 1874.
COLLECTION: " Challenger".

HIPPOMEDON Boeck

Hippomedon denticulatus (Bate) 1857 : 139 [*Anonyx denticulata*].

SYNTYPES: Reg. no. 1952 : 5 : 7 : 8–9 (6 specimens, alcohol).
LOCALITY: Moray Firth.
COLLECTION: Bate.

Hippomedon geelongi Stebbing 1888 : 635.

Holotype: Reg. no. 1889 : 5 : 15 : 12 (specimen in alcohol + 7 slides).
Locality: Sta. 161. Off Melbourne, Australia, 33 fm, 1 April 1874.
Collection: " Challenger".

Hippomedon holbolli var. abyssicola Sars 1885 : 142.

Syntype: Reg. no. 1911 : 11 : 8 : 12925 (1 specimen, alcohol).
Locality: Norwegian North Atlantic Expedition Sta. 40. 63° 22′ N 05° 29′ W, 2222 m, 18 July 1876.
Collection: Norman.

Hippomedon incisus Barnard 1930 : 325.

Syntypes: Reg. no. 1930 : 8 : 1 : 16–17 (2 specimens in alcohol + 1 slide).
Locality: Sta. 242. Off Akaroa Heads, New Zealand, 10 m, 2 April 1912.
Collection: " Terra Nova ".

Hippomedon longimanus (Stebbing) 1888 : 643 [*Platamon longimanus*].

Holotype: Reg. no. 1889 : 5 : 15 : 14 (part) (specimen in alcohol + 7 slides).
Paratype: Reg. no. 1889 : 5 : 15 : 14 (part) (1 specimen, alcohol).
Locality: Sta. 1. Off Cape Finisterre, Spain, 41° 58′ N 09° 42′ W, 1125 fm, 30 December 1872.
Collection: " Challenger ".

ICHNOPUS Costa

[*Ichnopus affinis*] Heller 1867 : 19 (transferred to *Ichnopus taurus* Costa by Della Valle 1893).

Syntype: Reg. no. 1911 : 11 : 8 : M655 (1 slide).
Locality: Adriatic Sea, 1866.
Collection: Norman.

[*Ichnopus serricrus*] Walker 1909 : 328 (transferred to *Ichnopus taurus* Costa by Spandl 1924).

Syntypes: Reg. no. 1909 : 1 : 29 : 14–16 (2 specimens, alcohol).
Localities: Coco Is., Cargados Islands, Indian Ocean, surface, 30 August 1905. Amirante Is., Indian Ocean, 22–85 fm, 11 October 1905.

Syntype: Reg. no. 1909 : 2 : 13 : 3 (1 slide).
Locality: Amirante Islands, Indian Ocean, 25–85 fm, 11 October 1905.
Collection: " Sealark " Expedition.

KERGUELENIA Stebbing

Kerguelenia antarctica Barnard 1930 : 318.

Syntypes: Reg. no. 1930 : 8 : 1 : 1–2 (2 specimens in alcohol + 1 slide).
Locality: Sta. 356. McMurdo Sound, Ross Sea, 92 m, 22 January 1913.
Collection: " Terra Nova ".

Kerguelenia compacta Stebbing 1888 : 1220.

SYNTYPES: Reg. no. 1889 : 5 : 15 : 159 (1 specimen in alcohol + 2 slides).
LOCALITIES: Off Christmas Harbour, Kerguelen, South Indian Ocean, 120 fm. Sta. 149H. Off Cumberland Bay, Kerguelen, South Indian Ocean, 127 fm, 29 January 1874.
COLLECTION: " Challenger ".

Kerguelenia palpalis Barnard 1932 : 28.

HOLOTYPE: Reg. no. 1936 : 11 : 2 : 1 (alcohol).
LOCALITY: Sta. 175. Bransfield Strait, South Shetland Islands, 63° 17′ S 59° 48′ W, 200 m, 2 March 1927.
COLLECTION: " Discovery " Committee.

LEPIDEPECREELLA Schellenberg

Lepidepecreella bidens (Barnard) 1930 : 321 [*Paracyclocaris bidens*].

SYNTYPES: Reg. no. 1930 : 8 : 1 : 5–8 (7 specimens in alcohol + 1 slide).
LOCALITY: Sta. 90. Off Three Kings Islands, New Zealand, 183 m, 25 July 1911.
COLLECTION: " Terra Nova ".

Lepidepecreella ovalis Barnard 1932 : 61.

SYNTYPES: Reg. no. 1936 : 11 : 2 : 329–330* (2 specimens, alcohol).
LOCALITY: Sta. 45. 2·7 miles S 85° E of Jason Light, South Georgia, 238–270 m, 6 April 1926.

SYNTYPES: Reg. no. 1936 : 11 : 2 : 331–333 (1 + 2 + 2 specimens, alcohol).
LOCALITIES: Sta. 42. Off Cumberland Bay, South Georgia, 120–204 m, 1 April 1926. Sta. 140. Stromness Harbour to Larsen Point, South Georgia, 122–136 m, 23 December 1926. Sta. WS 33. 54° 59′ S 35° 24′ W, 130 m, 21 December 1926.
COLLECTION: " Discovery " Committee.

LEPIDEPECREOIDES Barnard

Lepidepecreoides xenopus Barnard 1931 : 426.

SYNTYPE: Reg. no. 1936 : 11 : 2 : 334* (1 specimen, alcohol).
LOCALITY: Sta. 181. Schollaert Channel, Palmer Archipelago, Graham Land, 160–335 m, 12 March 1927.

SYNTYPES: Reg. no. 1936 : 11 : 2 : 335–336 (1 + 1 specimens, alcohol).
LOCALITIES: Sta. 177. 27 miles SW of Deception Island, South Shetland Islands, 1080 m, 5 March 1927. Sta. WS 33. 54° 59′ S 35° 24′ W, 130 m, 21 December 1926.
COLLECTION: " Discovery " Committee.

LEPIDEPECREUM Bate & Westwood

Lepidepecreum cingulatum Barnard 1932 : 60.

SYNTYPES: Reg. no. 1936 : 11 : 2 : 326–328 (4 specimens, alcohol).
LOCALITY: Sta. 165. Dove Strait, Signy Island, South Orkney Islands, 24–36 m, 18–20 February 1927.
COLLECTION: " Discovery " Committee.

Lepidepecreum foraminiferum Stebbing 1888: 686.

SYNTYPES: Reg. no. 1889 : 5 : 15 : 26 (4 specimens in alcohol + 6 slides).
LOCALITY: Sta. 149H. Off Cumberland Bay, Kerguelen, 127 fm, 29 January 1874.
COLLECTION: " Challenger ".

LYSIANASSA Milne Edwards

Lysianassa coelochir (Walker) 1904 : 243 [*Lysianax coelochir*].

SYNTYPES: Reg. no. 1905 : 2 : 18 : 17–18 (2 specimens, alcohol).
1905 : 2 : 18 : 312 (1 slide).
LOCALITY: Ceylon.
COLLECTION: Herdman.

Lysianassa urodus (Walker & Scott) 1903 : 220 [*Lysianax urodus*].

SYNTYPES: Reg. no. 1914 : 3 : 31 : 7–8 (2 specimens, alcohol).
LOCALITY: Abd-el-Kuri, Socotra.
DONOR: A. O. Walker.

Lysianassa variegata (Stimpson) 1856 : 394 [*Anonyx variegata*].

SYNTYPE: Reg. no. 68 : 107 (16) (1 specimen).
LOCALITY: Simon's Bay, Cape of Good Hope.
COLLECTION: Stimpson.

[*Lysianassa woodmasoni*] Giles 1890 : 68 (transferred to *Glycerina tenuicornis* (Haswell) by Pirlot 1936).

SYNTYPES: Reg. no. 1968 : 53 (1 slide).
LOCALITY: Macpherson's Strait, Andaman Islands, 17 fm.
COLLECTION: Giles.

METACYPHOCARIS Tattersall

Metacyphocaris helgae Tattersall 1906 : 29.

SYNTYPE: Reg. no. 1911 : 11 : 8 : 13692 (1 specimen, alcohol).
LOCALITY: 40 miles N by W of Eagle Island, Co. Mayo, Eire, 630 fm, February 1905.
COLLECTION: Norman.

Syntypes: Reg. no. 1947 : 11 : 4 : 11–13 (4 specimens, alcohol).
Locality: 40 miles N by W of Eagle Island, Co. Mayo, Eire, 750 fm, 11 August 1904.

Syntypes: Reg. no. 1947 : 11 : 4 : 14–16 (3 specimens, alcohol).
Locality: 53° 07′ N 15° 06′ W, 750 fm, 12 May 1905.

Syntype: Reg. no. 1947 : 11 : 4 : 17 (1 specimen, alcohol).
Locality: 50 miles N by W of Eagle Island, Co. Mayo, Eire, 600 fm, 20 May 1905.
Collection: Tattersall.

MICROLYSIAS Stebbing

Microlysias indica Barnard 1937 : 144.

Syntypes: Reg. no. 1938 : 1 : 3 : 19–22 (5 specimens, alcohol).
Locality: Sta. 53. South Arabian Coast, 19° 23′ N 57° 53′ E, 13·5 m, 2 November 1933.
Collection: " John Murray ".

Microlysias xenokeras Stebbing 1918 : 64.

Syntypes: Reg. no. 1928 : 12 : 1 : 2055–2061 (43 specimens, alcohol).
Locality: Vetch's Pier, Durban, South Africa, 2 fm, 9 July 1917. From sea squirt.
Donor: T. R. R. Stebbing.

NANNONYX Sars

Nannonyx integricauda (Stebbing) 1888 : 695 [*Ambasia integricauda*].

Holotype: Reg. no. 1889 : 5 : 15 : 29 (4 slides).
Locality: Sta. 149D. Royal Sound, Kerguelen, 28 fm, 20 January 1874.
Collection: " Challenger ".

Nannonyx spinimanus Walker 1895 : 292.

Syntype: Reg. no. 1914 : 3 : 31 : 9 (1 specimen, alcohol).
Locality: Pwll Fanog, Menai Strait, Wales, 10–12 fm, 2 April 1894.

Syntypes: Reg. no. 1907 : 4 : 8 : 5 (1 slide).
1908 : 3 : 10 : 7 (1 slide).
Locality: Menai Bridge, Wales, 7–10 fm, 31 May 1894.

Syntype: Reg. no. 1908 : 3 : 10 : 8 (1 slide).
Locality: Britannia Bridge, Menai Strait, Wales, 7–10 fm, 31 May 1894.
Donor: A. O. Walker.

The depths given here are those on the bottle or slide label. In his report Walker gives the depth as 5–8 fms.

NORMANION Bonnier

[*Normanion amblyops*] Sars 1895 : 674 (transferred to *Normanion quadrimanus* by Stebbing 1906).

SYNTYPES: Reg. no. 1911 : 11 : 8 : 12768–12772 (5 specimens, alcohol).
LOCALITY: Rødbjerget, Trondhjemsfjord, Norway, 200–300 fm. On skins of live *Gadus aeglefinus* [now *Melanogrammus aeglefinus* (L)] and *Spinax niger* [now *Etmopterus spinax* (L)].
COLLECTION: Norman.

Normanion quadrimanus (Bate and Westwood) 1868 : 503 [*Opis quadrimanus*].

SYNTYPE: Reg. no. 1911 : 11 : 8 : M654 (1 slide).
LOCALITY: Coast of Banffshire, 1864, collected Mr. Edward.
COLLECTION: Norman.

ONESIMOIDES Stebbing

Onesimoides carinatus Stebbing 1888 : 648.

HOLOTYPE: Reg. no. 1889 : 5 : 15 : 15 (specimen in alcohol + 6 slides).
LOCALITY: Sta. 184. Off the NE coast of Australia, 12° 08′ S 145° 10′ E, 1400 fm, 29 August 1874.
COLLECTION : " Challenger ".

ONISIMUS Boeck

Onisimus brevicaudatus Hansen 1887 : 216.

SYNTYPES: Reg. no. 1891 : 1 : 6 : 21–25 (5 specimens, alcohol).
LOCALITY: Kara Sea, 71° 13′ N, 110 m, " Dijmphna " Expedition.
DONOR: Copenhagen Museum.

SYNTYPES: Reg. no. 1911 : 11 : 8 : 13644–13648 (5 specimens, alcohol).
LOCALITY: Kara Sea, 71° 13′ N, 110 m, " Dijmphna " Expedition.
COLLECTION: Norman.

SYNTYPES: Reg. no. 1928 : 12 : 1 : 1623–1628 (7 specimens, alcohol).
LOCALITY: Kara Sea, 71° 13′ N, 110 m, " Dijmphna " Expedition.
COLLECTION: Stebbing.

Onisimus caricus Hansen 1887 : 214.

SYNTYPES: Reg. no. 1891 : 1 : 6 : 18–20 (3 specimens, alcohol).
LOCALITY: Kara Sea, " Dijmphna " Expedition.
DONOR: Copenhagen Museum.

SYNTYPES: Reg. no. 1911 : 11 : 8 : 13649–13652 (4 specimens, alcohol).
LOCALITY: Kara Sea, " Dijmphna " Expedition.
COLLECTION: Norman.

SYNTYPES: Reg. no. 1928 : 12 : 1 : 1615–1622 (part) (4 specimens, alcohol).
LOCALITY: Kara Sea, " Dijmphna " Expedition.
COLLECTION: Stebbing.

ORCHOMENE Boeck

Orchomene amblyops Sars 1890 : 65.

SYNTYPES: Reg. no. 1911 : 11 : 8 : 13087–13096 (11 specimens, alcohol).
LOCALITY: Trondhjemsfjord, Norway.
COLLECTION: Norman.

The absence of a date on the label of these specimens prevents absolute certainty as to their type status.

Orchomene batei Sars 1882 : 81.

SYNTYPES: Reg. no. 1911 : 11 : 8 : M731–732 (2 slides).
LOCALITY: West Norway.
COLLECTION: Norman.

The absence of a date, both on the slides and in the accession register, makes it impossible to be certain that these specimens are part of Sars' type series.

Orchomene goniops Walker 1906 : 455.

SYNTYPES: Reg. no. 1907 : 6 : 6 : 94–95 (2 specimens, alcohol).
1907 : 6 : 13 : 8 (1 slide).
LOCALITY: McMurdo Sound, Ross Sea, 21 August 1903.
COLLECTION: National Antarctic Expedition.

[*Orchomene musculosus*] Stebbing 1888 : 673 (transferred to *Orchomenella chilensis* (Heller) by Chilton 1912).

HOLOTYPE: Reg. no. 1889 : 5 : 15 : 22 (specimen in alcohol + 6 slides).
LOCALITY: Sta. 230. South of Japan, 26° 29′ N 137° 57′ E, surface, 5 April 1875.
COLLECTION: " Challenger ".

ORCHOMENELLA Sars

Orchomenella abyssorum (Stebbing) 1888 : 676 [*Orchomene abyssorum*].

HOLOTYPE: Reg. no. 1889 : 5 : 15 : 23 (alcohol, dissected).
LOCALITY: Sta. 323. South Atlantic Ocean, E of Buenos Aires, 35° 39′ S 50° 47′ W, 1900 fm.
COLLECTION: " Challenger ".

Orchomenella cavimanus (Stebbing) 1888 : 679 [*Orchomene cavimanus*].

HOLOTYPE: Reg. no. 1889 : 5 : 15 : 24 (part) (specimen in alcohol + 7 slides).
LOCALITY: Kerguelen, South Indian Ocean, no further data.

PARATYPES: Reg. no. 1889 : 5 : 15 : 24 (part) (1 + 1 specimens, alcohol).
LOCALITIES: Betsy Cove, Kerguelen, South Indian Ocean, surface. Sta. 149H. Off Cumberland Bay, Kerguelen, South Indian Ocean, 127 fm.
COLLECTION: " Challenger ".

Orchomenella chelipes Walker 1906 : 456.

SYNTYPES: Reg. no. 1907 : 6 : 6 : 136–143 (4 specimens, alcohol).
1907 : 6 : 13 : 9 (1 slide).
LOCALITY: McMurdo Sound, Ross Sea, 28 February 1902.
COLLECTION: National Antarctic Expedition.

Orchomenella chilensis (Heller) 1868 : 129 [*Anonyx chilensis*].

PARALECTOTYPES: Reg. no. 1966 : 8 : 14 : 1–24 (24 specimens, alcohol).
LOCALITY: Chile, " Novara " Expedition.
DONOR: Vienna Museum.

Orchomenella franklini Walker 1903 : 47.

HOLOTYPE: Reg. no. 1903 : 10 : 5 : 10 (alcohol).
LOCALITY: Franklin Island, Ross Sea.
COLLECTION: " Southern Cross ".

Orchomenella nodimanus (Walker) 1903 : 44 [*Orchomenopsis nodimanus*].

SYNTYPES: Reg. no. 1902 : 11 : 5 : 46–56 (ca 100 specimens in alcohol + 2 slides).
LOCALITY: Cape Adare, 26 fm, 4–5 November 1899.
COLLECTION: " Southern Cross".

Orchomenella pinguides Walker 1903 : 46.

SYNTYPES: Reg. no. 1902 : 11 : 5 : 39–45 (ca 130 specimens in alcohol + 3 slides).
LOCALITY: Cape Adare, 26 fm, 4–5 November 1899.
COLLECTION: " Southern Cross ".

Orchomenella plebs Hurley 1965 : 107.

PARATYPES: Reg. no. 1968 : 128 (12 specimens, alcohol).
LOCALITY: Sta. A. 32. White Island, Ross Ice Barrier, 15 November 1961.
DONOR: D. E. Hurley.

Orchomenella rotundifrons Barnard 1932 : 72.

SYNTYPES: Reg. no. 1936 : 11 : 2 : 523–529 (11 specimens, alcohol).
LOCALITY: Sta. 174. Deception Island, South Shetland Islands, 5–10 m, 28 February—2 March 1927.
COLLECTION: " Discovery " Committee.

[***ORCHOMENOPSIS*** Sars]

[*Orchomenopsis proxima*] Chevreux 1903 : 93 (transferred to *Orchomenella chilensis* (Heller) by Chilton 1912).

SYNTYPES: Reg. no. 1965 : 12 : 2 : 1–8 (16 specimens, alcohol).

LOCALITY: " Princesse Alice " Sta. 1138. Off the Cape Verde Islands, 16° 44′N 27° 08′ W, 692 m, 21–22 July 1901.
DONOR: Monaco Museum.

[*Orchomenopsis rossi*] Walker 1903 : 45 (transferred to *Orchomenella chilensis* (Heller) by Chilton 1912).

SYNTYPES: Reg. no. 1902 : 11 : 5 : 85–90 (31 specimens in alcohol + 1 slide).
LOCALITY: Ross Sea, 78° 35′ S, near surface, 18 February 1900.
COLLECTION: " Southern Cross ".

PERRIERELLA Chevreux & Bouvier

Perrierella audouiniana (Bate) 1857 : 138 [*Lysianassa audouiniana*].

HOLOTYPE: Reg. no. 1952 : 5 : 7 : 1 (alcohol).
LOCALITY: Plymouth Sound, England.
COLLECTION: Bate.

PODOPRION Chevreux

Podoprion bolivari Chevreux 1891 : 6.

SYNTYPES: Reg. no. 1907 : 12 : 2 : 100–103 (4 specimens, alcohol).
LOCALITY: Vigo Bay, Spain.
DONOR: University College, Dundee.

SYNTYPES: Reg. no. 1911 : 11 : 8 : 13660 (1 specimen, alcohol).
1911 : 11 : 8 : 13661–13665 (5 specimens, alcohol).
LOCALITY: Vigo Bay, Spain, 20 m.
COLLECTION: Norman.

SYNTYPES: Reg. no. 1928 : 12 : 1 : 1602–1604 (4 specimens, alcohol).
LOCALITY: Vigo Bay, Spain.
COLLECTION: Stebbing.

PODOPRIONIDES Walker

Podoprionides incerta Walker 1906 : 457.
HOLOTYPE: Reg. no. 1907 : 6 : 6 : 200 (1 specimen, alcohol).
1907 : 6 : 13 : 10 (1 slide).
LOCALITY: Hole 12, Winter Quarters, McMurdo Sound, Ross Sea, 29 August 1902.
COLLECTION: National Antarctic Expedition.

PSEUDALIBROTUS Della Valle

Pseudalibrotus caspius Sars 1896 : 422.

SYNTYPES: Reg. no. 1911 : 11 : 8 : 13599–13600 (2 specimens, alcohol).
LOCALITY: Central Caspian Sea, 250 fm.
COLLECTION: Norman.

PSEUDORCHOMENE Schellenberg

Pseudorchomene coatsi (Chilton) 1912 : 477 [*Orchomenopsis coatsi*].

SYNTYPES: Reg. no. 1912 : 10 : 5 : 4–18 (15 specimens, alcohol).
LOCALITY: Sta. 411. Off Coats Land, 74° 01′ S 22° 00′ W, 161 fm, 12 March 1904.
COLLECTION: " Scotia ".
DONOR: Dr. W. S. Bruce.

SYNTYPES: Reg. no. 1912 : 10 : 14 : 49–53 (7 specimens, alcohol).
LOCALITY: Sta. 411. Off Coats Land, 74° 01′ S 22° 00′ W, 161 fm, 12 March 1904.
COLLECTION: " Scotia ".
DONOR: Prof. C. Chilton.

SCOPELOCHEIRUS Bate

Scopelocheirus crenatus Bate 1857 : 138.

SYNTYPES: Reg. no. 1952 : 5 : 7 : 13 (26 specimens, alcohol).
LOCALITY: Plymouth Sound.
COLLECTION: Bate.

SHACKLETONIA Barnard

Shackletonia robusta Barnard 1932 : 29.

HOLOTYPE: Reg. no. 1936 : 11 : 2 : 2 (alcohol).
LOCALITY: Sta. 170. Off Cape Bowles, Clarence Island, South Shetland Islands, 61° 25′ S 53° 46′ W, 342 m, 23 February 1927.

PARATYPE: Reg. no. 1936 : 11 : 2 : 3 (1 specimen, alcohol).
LOCALITY: Sta. 123. Off mouth of Cumberland Bay, South Georgia, 230–250 m, 15 December 1926.
COLLECTION: " Discovery " Committee.

SOCARNELLA Walker

Socarnella bonnieri Walker 1904 : 239.

SYNTYPES: Reg. no. 1905 : 2 : 18 : 306–307 (2 slides).
LOCALITY: Galle, Ceylon. On reef with ascidians.
COLLECTION: Herdman.

SOCARNES Boeck

Socarnes erythrophthalmus Robertson 1892 : 200.

SYNTYPES: Reg. no. 1911 : 11 : 8 : 12714–12728 (15 specimens, alcohol).
1911 : 11 : 8 : M682 (1 slide).
LOCALITY: Cumbrae, Firth of Clyde, Scotland, 1888.
COLLECTION: Norman.

SOCARNOIDES Stebbing

Socarnoides kergueleni Stebbing 1888 : 691.

SYNTYPES: Reg. no. 1889 : 5 : 15 : 27 (2 specimens in alcohol + 5 slides).
LOCALITY: Sta. 149E. Greenland Harbour, Kerguelen, South Indian Ocean, 30 fm, 21 January 1874.

SYNTYPE: Reg. no. 1889 : 5 : 15 : 28 (1 specimen in alcohol + 2 slides).
LOCALITY: Sta. 149H. Off Cumberland Bay, Kerguelen, South Indian Ocean, 127 fm, 29 January 1874.
COLLECTION: " Challenger ".

SOCARNOPSIS Chevreux

Socarnopsis crenulata Chevreux 1910 : 165.

SYNTYPES: Reg. no. 1912 : 4 : 4 : 1–4 (4 specimens, alcohol).
LOCALITY: Bougie, Algeria.
DONOR: E. Chevreux.

SOPHROSYNE Stebbing

Sophrosyne murrayi Stebbing 1888 : 652.

HOLOTYPE: Reg. no. 1889 : 5 : 15 : 16 (specimen in alcohol + 2 slides).
LOCALITY: Off Christmas Harbour, Kerguelen, South Indian Ocean.
COLLECTION: " Challenger ".

STOMACONTION Stebbing

Stomacontion insigne Barnard 1932 : 33.

HOLOTYPE: Reg. no. 1936 : 11 : 2 : 9 (alcohol).
1936 : 11 : 2 : 3608 (alcohol, mouth parts relaxed from slide.)
LOCALITY: Sta. 160. Near Shag Rocks, South Atlantic Ocean, 53° 43′ S 40° 57′ W, 177 m, 7 February 1927.
COLLECTION: " Discovery " Committee.

Stomacontion kergueleni (Stebbing) 1888 : 720 [*Acontiostoma kergueleni*].

HOLOTYPE: Reg. no. 1889 : 5 : 15 : 36 (4 slides).
LOCALITY: Sta. 149D. Royal Sound, Kerguelen, South Indian Ocean, 28 fm, 20 January 1874.
COLLECTION: " Challenger ".

Stomacontion pepinii (Stebbing) 1888 : 716 [*Acontiostoma pepinii*].

SYNTYPES: Reg. no. 1889 : 5 : 15 : 35 (2 specimens in alcohol + 5 slides).
LOCALITY: Sta. 149B. Royal Sound, Kerguelen, South Indian Ocean, 28 fm, 20 January 1874.
COLLECTION: " Challenger ".

TMETONYX Stebbing

Tmetonyx bruuni Reid 1951 : 196.

PARATYPES: Reg. no. 1961 : 8 : 1 : 487–495 (9 specimens, alcohol).
LOCALITY: Sta. 160. Off Bathurst, Gambia, West Africa, 14 m, 24 April 1946.
COLLECTION: " Atlantide ".

Tmetonyx cicadoides (Stebbing) 1888 : 612 [*Anonyx cicadoides*].

SYNTYPES: Reg. no. 1889 : 5 : 15 : 3–5 (16 specimens in alcohol + 17 slides).
LOCALITIES: Sta. 149. Accessible Bay, Kerguelen, South Indian Ocean, 20 fm, 9 January 1874. Sta. 149D. Royal Sound, Kerguelen, South Indian Ocean, 28 fm, 20 January 1874. Sta. 149H. Off Cumberland Bay, Kerguelen, South Indian Ocean, 127 fm, 29 January 1874.
COLLECTION: " Challenger ".

Tmetonyx longitelson Barnard 1932 : 54.

SYNTYPES: Reg. no. 1936 : 11 : 2 : 317–319 (3 specimens, alcohol).
LOCALITY: Sta. 159. 53° 52′ S 36° 08′ W, 160 m, 21 January 1927.
COLLECTION: " Discovery " Committee.

Tmetonyx miersi (Stebbing) 1888 : 631 [*Hippomedon miersi*].

HOLOTYPE: Reg. no. 1889 : 5 : 15 : 11 (1 specimen in alcohol + 7 slides).
LOCALITY: Sta. 162. Off East Moncoeur Island, Victoria, Australia, 39° 10′ S 146° 37′ E, 38 fm, 2 April 1874.
COLLECTION: " Challenger ".

Tmetonyx nobilis (Stimpson) 1853 : 50 [*Anonyx nobilis*].

SYNTYPES: Reg. no. 68 : 107 (9, 23) (3 + 2 specimens, alcohol).
LOCALITY: Nantucket Island, Mass., U.S.A.
COLLECTION: Stimpson.

Tmetonyx stebbingi (Walker) 1903 : 52 [*Hoplonyx stebbingi*].

SYNTYPE: Reg. no. 1902 : 11 : 5 : 126 (1 specimen, alcohol).
LOCALITY: Cape Adare, South Victoria Land.

SYNTYPES: Reg. no. 1903 : 10 : 5 : 11–12 (2 specimens in alcohol + 1 slide).
LOCALITY: Cape Adare, South Victoria Land, 26 fm, 4–5 November 1899.
COLLECTION: " Southern Cross ".

Barnard (1958) on the authority of Chilton (1912) listed *Hoplonyx stebbingi* Walker under *Tryphosites*. It has since been shown (Hurley 1965*a*) that two species were present, *Tmetonyx stebbingi* (Walker) and *Tryphosites capadarei* Hurley.

TRISCHIZOSTOMA Boeck

Trischizostoma serratum Barnard 1925 : 320.

SYNTYPE: Reg. no. 1928 : 4 : 13 : 13 (1 specimen, alcohol).
LOCALITY: Off Natal, South Africa.
DONOR: South African Museum.

TRYPHOSA Boeck

Tryphosa adarei Walker 1903 : 49.

SYNTYPES: Reg. no. 1902 : 11 : 5 : 127–135 (12 specimens in alcohol + 2 slides).
1903 : 10 : 5 : 16 (2 specimens, alcohol).
LOCALITY: Cape Adare, South Victoria Land, 26 fm, 4–5 November 1899.
COLLECTION: " Southern Cross ".

Tryphosa analogica Barnard 1932 : 52.

SYNTYPES: Reg. no. 1936 : 11 : 2 : 298–300* (3 specimens, alcohol).
LOCALITY: Sta. WS 25. Undine Harbour, South Georgia, 18–27 m, 17 December 1926.

SYNTYPES: Reg. no. 1936 : 11 : 2 : 301–305 (3 + 3 + 1 specimens, alcohol).
LOCALITIES: Sta. 144. 53° 48′ S 35° 37′ W, 728 m, 8 January 1927. Sta. 156. 53° 51′ S 36° 21′ W, 200–236 m, 20 January 1927. Sta. 159. 53° 52′ S 36° 08′ W, 160 m, 21 January 1927.
COLLECTION: " Discovery " Committee.

Tryphosa angulata Sars 1891 : 78.

SYNTYPES: Reg. no. 1911 : 11 : 8 : 13257–13261 (5 specimens, alcohol).
LOCALITY: Trondhjemsfjord, Norway.
COLLECTION: Norman.
No date is recorded on the bottle label or in the accession register, and without this, the type status of these specimens cannot be confirmed.

[*Tryphosa antennipotens*] Stebbing 1888 : 617 (transferred to *Uristes gigas* Dana by Stebbing 1906).

HOLOTYPE: Reg. no. 1889 : 5 : 15 : 6 (1 specimen in alcohol + 6 slides).
LOCALITY: Sta. 150. Off Heard Island, South Indian Ocean, 52° 04′S 71° 22′E, 150 fm, 2 February 1874.
COLLECTION: " Challenger ".

Tryphosa castellata Barnard 1932 : 53.

SYNTYPES: Reg. no. 1936 : 11 : 2 : 306–307 (2 specimens, alcohol).
LOCALITY: Sta. 222. St. Martin's Cove, Hermite Island, Cape Horn, 30–35 m, 23–24 April 1927.
COLLECTION: " Discovery " Committee.

[*Tryphosa ciliata* Sars] 1882 : 81 (transferred to *Orchomenella nana* (Krøyer) by Bonnier 1893).

SYNTYPE: Reg. no. 1911 : 11 : 8 : M752 (1 slide).
LOCALITY: South Norway.
COLLECTION: Norman.
This slide has no date on its label, so it is not possible to confirm the type status of the specimen.

Tryphosa cucullata Walker 1904 : 244.

Holotype: Reg. no. 1905 : 2 : 18 : 25 (alcohol).
Locality: Kondatchi Paar, Ceylon, 17 November 1902.
Collection: Herdman.

Tryphosa kergueleni (Miers) 1875 : 74 [*Lysianassa kergueleni*].

Syntypes: Reg. no. 76 : 27 (6 specimens, alcohol).
Locality: Royal Sound, Kerguelen, South Indian Ocean.
Donor: Rev. A. E. Eaton.

Tryphosa major Barnard 1932 : 50.

Syntypes: Reg. no. 1936 : 11 : 2 : 261–263* (4 specimens, alcohol).
Locality: Sta. 170. Off Cape Bowles, Clarence Island, South Shetland Islands, 61° 25′ S 53° 46′ W, 342 m, 23 February 1927.

Syntypes: Reg. no. 1936 : 11 : 2 : 264–270 (7 + 3 specimens, alcohol).
Localities: Sta. 159. 53° 52′ S 36° 08′ W, 160 m, 21 January 1927. Sta. 175. Bransfield Strait, South Shetland Islands, 63° 17′ S 59° 48′ W, 200 m, 2 March 1927.
Collection: " Discovery " Committee.

Tryphosa murrayi Walker 1903 : 50.

Syntypes: Reg. no. 1902 : 11 : 5 : 136–137 (2 specimens, alcohol).
Locality: Cape Adare, South Victoria Land.
Collection: " Southern Cross ".

Tryphosa triangularis Barnard 1932 : 51.

Syntypes: Reg. no. 1936 : 11 : 2 : 275–283* (10 specimens in alcohol + 5 slides).
Locality: Sta. 159. 53° 52′ S 36° 08′ W, 160 m, 21 January 1927.

Syntypes: Reg. no. 1936 : 11 : 2 : 284–297 (2 + 6 + 3 + 8 + 4 specimens, alcohol).
Localities: Sta. 140. Stromness Harbour to Larsen Point, South Georgia, 122–136 m, 23 December 1926. Sta. 141. East Cumberland Bay, South Georgia, 17–27 m, 29 December 1926. Sta. 144. Off entrance of Stromness Harbour, South Georgia, 155–178 m, 5 January 1927. Sta. 145. Stromness Harbour, South Georgia, 26–35 m, 7 January 1927. Sta. WS 25. Undine Harbour, South Georgia, 18–27 m, 17 December 1926.
Collection: " Discovery " Committee.

Tryphosa trigonica (Stebbing) 1888 : 630 [*Hippomedon trigonicus*].

Syntype: Reg. no. 1889 : 5 : 15 : 10 (part) (1 specimen in alcohol + 5 slides).
Locality: Kerguelen, South Indian Ocean, no further data.

Syntypes: Reg. no. 1889 : 5 : 15 : 10 (part) (4 specimens, alcohol).
Locality: Kerguelen, South Indian Ocean, 120 fm.
Collection: " Challenger ".

SYNTYPES: Reg. no. 1928 : 12 : 1 : 1719–1721 (3 specimens, alcohol).
LOCALITY: Kerguelen, South Indian Ocean, 30 fm.
COLLECTION: Stebbing.

TRYPHOSELLA Bonnier

Tryphosella albina Barnard 1932 : 48.

HOLOTYPE: Reg. no. 1936 : 11 : 2 : 249 (alcohol).
LOCALITY: Sta. 170. Off Cape Bowles, Clarence Island, 61° 25′ S 53° 46′ W, 342 m, 23 February 1927.
COLLECTION: " Discovery " Committee.

Tryphosella barbatipes (Stebbing) 1888 : 621 [*Tryphosa barbatipes*].

SYNTYPES: Reg. no. 1889 : 5 : 15 : 7 (2 specimens in alcohol + 8 slides).
LOCALITY: Sta. 149 H. Off Cumberland Bay, Kerguelen, South Indian Ocean, 127 fm, 29 January 1874.
COLLECTION: " Challenger ".

TRYPHOSITES Sars

Tryphosites capadarei Hurley 1965a : 177.

HOLOTYPE: Reg. no. 1965 : 12 : 2 : 9 (alcohol).
LOCALITY: Cape Adare, South Victoria Land, 26 fm, 4–5 November 1899.
COLLECTION: " Southern Cross ".

Tryphosites chevreuxi Stebbing 1914 : 355.

SYNTYPES: Reg. no. 1928 : 12 : 1 : 1729–1737 (9 specimens, alcohol).
LOCALITY: Roy Cove, Falkland Islands, 8 fm.
COLLECTION: Stebbing.

VALETTIA Stebbing

Valettia coheres Stebbing 1888 : 724.

HOLOTYPE: Reg. no. 1889 : 5 : 15 : 37 (specimen in alcohol + 4 slides).
LOCALITY: Sta. 156. Antarctic Ocean, 62° 26′ S 95° 44′ E, 1975 fm, 26 February 1874.
COLLECTION: " Challenger ".

WALDECKIA Chevreux

Waldeckia kroyeri (White) 1847 : 124 [*Ephippiphora kroyeri*].

SYNTYPE: Reg. no. 45 : 47 (1 specimen, dry).
LOCALITY: Tasmania.
DONOR: Admiralty.

Family **STEGOCEPHALIDAE**

ANDANIA Boeck

[*Andania abyssorum*] Stebbing 1888 : 739 (transferred to *Andaniotes corpulentus* (Thomson) by Stebbing 1897).

HOLOTYPE: Reg. no. 1889 : 5 : 15 : 42 (7 slides).
LOCALITY: Sta. 168. Off New Zealand, 40° 28′ S 177° 43′ E, 1100 fm, 8 July 1874.
COLLECTION: " Challenger ".

ANDANIEXIS Stebbing

Andaniexis australis Barnard 1932 : 76.

SYNTYPE: Reg. no. 1936 : 11 : 2 : 588–591* (4 specimens, alcohol).
LOCALITY: Sta. 87. 33° 53′ S 09° 26′ E, 1000(–0) m, 25 June 1926.

SYNTYPE: Reg. no. 1936 : 11 : 2 : 592 (1 specimen, alcohol).
LOCALITY: Sta. 89. 34° 05′ S 16° 00′ E 1000(–0) m, 28 June 1926.
COLLECTION: " Discovery " Committee.

ANDANIOTES Stebbing

Andaniotes linearis Barnard 1932 : 80.

SYNTYPES: Reg. no. 1936 : 11 : 2 : 644–648* (6 specimens, alcohol).
LOCALITY: Sta. 156. 53° 51′ S 36° 21′ W, 200–236 m, 20 January 1927.

SYNTYPES: Reg. no. 1936 : 11 : 2 : 649–656 (1 + 3 + 2 + 1 + 1 + 1 + 2 specimens, alcohol).
LOCALITIES: Sta. 39. East Cumberland Bay, South Georgia, 179–235 m, 25 March 1926. Sta. 42. Off entrance of Cumberland Bay, South Georgia, 120–204 m, 1 April 1926. Sta. 144. Off entrance of Stromness Harbour, South Georgia, 155–178 m, 5 January 1927. Sta. 148. Off Cape Saunders, South Georgia, 132–148m, 9 January 1927. Sta. 149. Entrance of East Cumberland Bay, South Georgia, 200–234 m, 10 January 1927. Sta. 175. Bransfield Strait, South Shetland Islands, 63° 17′ S 59° 48′ W, 200 m, 2 March 1927. Sta. 190. Bismarck Strait, Palmer Archipelago, 90–130 m, 24 March 1927.
COLLECTION: " Discovery " Committee.

Andaniotes simplex Barnard 1930 : 328.

SYNTYPES: Reg. no. 1930 : 8 : 1 : 92–94 (3 specimens in alcohol + 1 slide).
LOCALITY: Sta. 90. Off Three Kings Islands, New Zealand, 183 m, 25 August 1911.
COLLECTION: " Terra Nova ".

BATHYSTEGOCEPHALUS Schellenberg

Bathystegocephalus globosus (Walker) 1909 : 329 [*Stegocephalus globosus*].

SYNTYPES: Reg. no. 1909 : 1 : 29 : 17–31 (part) (2 + 17 + 2 specimens, alcohol).
LOCALITIES: Indian Ocean, 200 fm, 200 fm, and 750 fm, 16 October 1905.

SYNTYPES: Reg. no. 1909 : 1 : 29 : 17–31 (part) (2 specimens, alcohol).
LOCALITY: Indian Ocean, 250–500 fm, 17 September 1905.

SYNTYPE: Reg. no. 1909 : 2 : 13 : 4 (1 slide).
LOCALITY: Indian Ocean, 200 fm, 16 October 1905.
COLLECTION: " Sealark ".

SYNTYPES: Reg. no. 1925 : 9 : 8 : 122–123 (2 specimens, alcohol).
LOCALITY: Indian Ocean, 200 fm, 16 October 1905.
COLLECTION: Walker.

EUANDANIA Stebbing

Euandania gigantea (Stebbing) 1888 : 730 [*Andania gigantea*].

SYNTYPE: Reg. no. 1889 : 5 : 15 : 39 (1 specimen, alcohol).
LOCALITY: Sta. 146. Near Marion Island, South Indian Ocean, 46° 46′ S 45° 31′E, 1375 fm, 29 December 1873.

SYNTYPE: Reg. no. 1889 : 5 : 15 : 40 (1 specimen in alcohol + 13 slides).
LOCALITY: Sta. 147. East of Marion Island, South Indian Ocean, 46° 16′S 48° 27′ E, 1600 fm, 30 December 1873.
COLLECTION: " Challenger ".

PARANDANIA Stebbing

Parandania boecki (Stebbing) 1888 : 735 [*Andania boecki*].

HOLOTYPE: Reg. no. 1889 : 5 : 15 : 41 (specimen in alcohol + 8 slides).
LOCALITY: Sta. 120. Off Pernambuco, 08° 37′ S 34° 28′ W, 675 fm, 9 September 1873.
COLLECTION: " Challenger ".

PHIPPSIA Stebbing

Phippsia gibbosa (Sars) 1882 : 85 [*Stegocephalus gibbosus*].

SYNTYPE: Reg. no. 1911 : 11 : 8 : M981 (1 slide).
LOCALITY: West Norway.
COLLECTION: Norman.

The absence of date and precise locality leaves some doubt as to the validity of the type status of this specimen.

PHIPPSIELLA Schellenberg

Phippsiella rostrata Barnard 1932 : 76.

SYNTYPES: Reg. no. 1936 : 11 : 2 : 585–587 (3 specimens, alcohol).
LOCALITY: Sta. 158. 53° 51′ S 36° 21′W, 200–236 m, 21 January 1927.
COLLECTION: " Discovery " Committee.

STEGOCEPHALOIDES Sars

Stegocephaloides attingens Barnard 1916 : 131.

SYNTYPES: Reg. no. 1928 : 4 : 13 : 41–44 (4 specimens, alcohol).
LOCALITY: South Africa.
DONOR: South African Museum.

Stegocephaloides auratus (Sars) 1882 : 86 [*Stegocephalus auratus*].

SYNTYPE: Reg. no. 1911 : 11 : 8 : M980 (1 slide).
LOCALITY: Finmark.
COLLECTION: Norman.

The validity of the type status of this specimen is in doubt. The locality given in the original description (Sars 1882) is " Norvegiae occidentalis ". Later, (Sars 1891) this is repeated, but three separate localities are given, of which Magerø is in Finmark.

Stegocephaloides australis Barnard 1916 : 129.

SYNTYPES: Reg. no. 1928 : 4 : 13 : 45–48 (4 specimens, alcohol).
LOCALITY: South Africa.
DONOR: South African Museum.

Family **AMPELISCIDAE**

AMPELISCA Krøyer

Ampelisca abyssicola Stebbing 1888 : 1047.

HOLOTYPE: Reg. no. 1889 : 5 : 15 : 121 (specimen in alcohol + 6 slides).
LOCALITY: Sta. 24. Off Culebra Island, St. Thomas, Virgin Islands, 18° 39′ N 65° 05′ W, 390 fm, 25 March 1873.
COLLECTION: " Challenger ".

Ampelisca acinaces Stebbing 1888 : 1036.

HOLOTYPE: Reg. no. 1889 : 5 : 15 : 119 (specimen in alcohol + 7 slides).
LOCALITY: Sta. 163B. Port Jackson, Sydney, Australia, 35 fm, 3 June 1874. (Slide label gives locality as Sta. 163A, 30 fm.)
COLLECTION: " Challenger ".

Ampelisca amblyops Sars 1891 : 180.

SYNTYPES: Reg. no. 1911 : 11 : 8 : 15027 (2 specimens, alcohol).
LOCALITY: Christianiafjord, Norway.
COLLECTION: Norman.

Ampelisca anomala Sars 1882 : 108.

SYNTYPES: Reg. no. 1911 : 11 : 8 : 15025–15026 (2 specimens, alcohol).
LOCALITY: West Norway.
COLLECTION: Norman.

Considerable doubt must be attached to the type status of these specimens as Sars had only two examples when he descibed the species.

Ampelisca birulai Brüggen 1909 : 17.

SYNTYPES: Reg. no. 1936 : 3 : 18 : 120–122 (3 specimens, alcohol).
LOCALITY: Siberian Sea.
DONOR: Academy of Sciences, Leningrad.

Ampelisca brachyceras Walker 1904 : 251.
SYNTYPES: Reg. no. 1905 : 2 : 18 : 42 (1 specimen, alcohol).
1905 : 2 : 18 : 322 (1 slide).
LOCALITY: Ceylon, November, 1902.
COLLECTION: Herdman.

Ampelisca bransfieldi Barnard 1932 : 83.

SYNTYPES: Reg. no. 1936 : 11 : 2 : 708–709 (2 specimens, alcohol).
LOCALITY: Sta. 177. 27 miles SW of Deception Island, South Shetland Islands, 1080 m, 5 March 1927.
COLLECTION: " Discovery " Committee.

Ampelisca brevicornis var. *cavicoxa* Reid 1951 : 208.

SYNTYPES: Reg. no. 1961 : 8 : 1 : 503–504 (2 specimens, alcohol).
LOCALITY: Sta. 161. Off Bathurst, Gambia, 18 m, 27 July 1946.
COLLECTION: " Atlantide ".

Ampelisca byblisoides Barnard 1925 : 335.

SYNTYPES: Reg. no. 1928 : 4 : 13 : 54–57 (4 specimens, alcohol).
LOCALITY: South Africa.
DONOR: South African Museum.

[*Ampelisca chevreuxi*] Walker 1904 : 254 (transferred to *Ampelisca zamboangae* Stebbing by Pirlot 1936).

HOLOTYPE: Reg. no. 1905 : 2 : 18 : 50 (alcohol).
1905 : 2 : 18 : 329 (1 slide).
LOCALITY: 12 miles W of Vankala, Ceylon, 7½–9 fm, 6 March 1902.
COLLECTION: Herdman.

Ampelisca chiltoni Stebbing 1888 : 1042.

SYNTYPES: Reg. no. 1889 : 5 : 15 : 120 (4 specimens in alcohol + 8 slides).
LOCALITY: Sta. 167. Off New Zealand, 39° 32′ S 171° 48′ E, 150 fm, 24 June 1874. (slide label gives Sta. 167A, 10 fm.)
COLLECTION: " Challenger ".

Sta. 167A is not mentioned in Stebbing's report. It was collected in Queen Charlotte Sound, South Island, New Zealand, on 27 June 1874. This locality is ca. 280 km SE of the position of Sta. 167.

Ampelisca compacta Norman 1882 : 688.

HOLOTYPE: Reg. no. 1911 : 11 : 8 : M963 (1 slide).
LOCALITY: " Knight Errant " Sta. 7. Off Lewis, Scotland, 59° 37′ N 07° 19′ W, 530 fm, 11 August 1880.
COLLECTION: Norman.

Ampelisca cyclops Walker 1904 : 253.

SYNTYPES: Reg. no. 1905 : 2 : 18 : 49 (2 specimens, alcohol).
1905 : 2 : 18 : 327–328 (2 slides).
LOCALITY: Ceylon.
COLLECTION: Herdman.

Ampelisca fusca Stebbing 1888 : 1052.

SYNTYPES: Reg. no. 1889 : 5 : 15 : 122 (3 specimens in alcohol + 7 slides).
LOCALITY: Sta. 142. Off Cape Agulhas, South Africa, 35° 04′ S 18° 37′ E, 150 fm, 18 December 1873.
COLLECTION: " Challenger ".

Ampelisca hemicryptops Barnard 1930 : 329.

SYNTYPES: Reg. no. 1930 : 8 : 1 : 105–108 (4 specimens, alcohol).
LOCALITY: Sta. 339. McMurdo Sound, Ross Sea, 256 m, 24 January 1912.

SYNTYPES: Reg. no. 1930 : 8 : 1 : 109–113 (3 + 2 specimens, alcohol).
LOCALITIES: Sta. 194. Oates Land, Antarctica, 329–366 m, 22 February 1911. Sta. 314. McMurdo Sound, Ross Sea, 406–441 m, 23 January 1912.
COLLECTION: " Terra Nova ".

[*Ampelisca ingens*] Bate 1862 : 92 (transferred to *Ampelisca eschrichti* Krøyer by Sars 1891).

SYNTYPES: Reg. no. 68 : 107 (6) (3 specimens, alcohol).
LOCALITY: Grand Manan, New Brunswick, Canada.
COLLECTION: Stimpson.

Ampelisca japonica Bate 1862 : 94.

HOLOTYPE: Reg. no. 68 : 107 (18) (alcohol).
LOCALITY: Japan.
COLLECTION: Stimpson.

Ampelisca limicola (Stimpson) 1853 : 57 [*Pseudophthalmus limicolus*].

Syntype: Reg. no. 68 : 107 (19) (1 specimen, alcohol).
Locality: Charleston Harbour, S. Carolina, U.S.A.
Collection: Stimpson.

Ampelisca palmata Barnard 1916 : 136.

Syntypes: Reg. no. 1928 : 4 : 13 : 49–53 (10 specimens, alcohol).
Locality: South Africa.
Donor: South African Museum.

Ampelisca pusilla Sars 1891 : 181.

Syntypes: Reg. no. 1911 : 11 : 8 : 15033–15042 (14 specimens, alcohol).
Locality: Trondhjemsfjord, Norway.
Collection: Norman.
Probably type material.

Ampelisca sarsi Chevreux 1888 : 666.

Syntypes: Reg. no. 1911 : 11 : 8 : 15068–15069 (2 specimens, alcohol).
Locality: Le Croisic, France.
Collection: Norman.

Ampelisca scabripes Walker 1904 : 250.

Syntypes: Reg. no. 1905 : 2 : 18 : 39–41 (3 specimens, alcohol).
Locality: Periya Paar, Ceylon.

Syntypes: Reg. no. 1905 : 2 : 18 : 321 (1 slide).
Locality: Ceylon.
Collection: Herdman.

Ampelisca statenensis Barnard 1932 : 84.

Holotype: Reg. no. 1936 : 11 : 2 : 710 (alcohol).
Locality: Sta. WS 88, 54° 00′ S 64° 57′ W, 118 fm, 6 April 1927.
Collection: " Discovery " Committee.

Ampelisca tridens Walker 1904 : 249.

Syntypes: Reg. no. 1905 : 2 : 18 : 33–38 (7 specimens, alcohol).
Locality: Sta. LVIII, Gulf of Manaar, Ceylon, 10 March 1902.

Syntypes: Reg. no. 1905 : 2 : 18 : 318–320 (3 slides).
Locality: Ceylon.
Collection: Herdman.

Syntypes: Reg. no. 1925 : 9 : 8 : 163–172 (13 specimens, alcohol).
1925 : 9 : 8 : 176–181 (6 specimens, alcohol).
Locality: Sta. XXXII, Ceylon.

SYNTYPES: Reg. no. 1925 : 9 : 8 : 173–175 (3 specimens, alcohol).
1925 : 9 : 8 : 182–191 (ca. 50 specimens, alcohol).
1925 : 9 : 8 : 192–195 (4 specimens, alcohol).
LOCALITY: Ceylon.

SYNTYPES: Reg. no. 1925 : 9 : 8 : 196–205 (15 specimens, alcohol).
LOCALITY: E. Cheval Paar, Ceylon, November 1902.
COLLECTION: Walker.

Ampelisca zamboangae Stebbing 1888 : 1057.

HOLOTYPE: Reg. no. 1889 : 5 : 15 : 123 (4 slides).
LOCALITY: Off Samboangan, Philippine Islands, surface, 18 February 1875.
COLLECTION: " Challenger ".

BYBLIS Boeck

Byblis abyssi Sars 1879 : 456.

SYNTYPE: Reg. no. 1911 : 11 : 8 : 15133 (1 specimen, alcohol).
LOCALITY: Norwegian North Atlantic Expedition Sta. 31. Norwegian Sea. 63° 10′ N 05° 00′ E, 763 m, 29 June 1876.
COLLECTION: Norman.

Byblis affinis Sars 1891 : 186.

SYNTYPES: Reg. no. 1911 : 11 : 8 : 15126–15131 (7 specimens, alcohol).
LOCALITY: Trondhjemsfjord, Norway, 40–60 fm.
COLLECTION: Norman.

Byblis erythrops Sars 1882 : 109.

SYNTYPE: Reg. no. 1911 : 11 : 8 : M969 (1 slide).
LOCALITY: Bejan, West Norway.
COLLECTION: Norman.

Byblis lepta (Giles) 1888 : 223 [*Ampelisca lepta*].

SYNTYPES: Reg. no. 87 : 14 (ca. 40 specimens, alcohol).
1909 : 4 : 3 : 1 (3 slides).
LOCALITY: Swatch-of-no-Ground, Bay of Bengal, 107 fm.
COLLECTION: Giles.

Byblis longicornis Sars 1891 : 185.

SYNTYPE: Reg. no. 1911 : 11 : 8 : 15132 (1 specimen, alcohol).
LOCALITY: Norwegian North Atlantic Expedition Sta. 260. Porsangerfjord, Norway, 70° 55′ N 26° 11′ E, 232 m, 25 June 1878.
COLLECTION: Norman.

BYBLISOIDES Barnard

Byblisoides juxtacornis Barnard 1931 : 426.

Syntypes: Reg. no. 1936 : 11 : 2 : 735–740* (8 specimens, alcohol).
Locality: Sta. 181. Schollaert Channel, Palmer Archipelago, Graham Land, 278–500 m, 12 March 1927.

Syntype: Reg. no. 1936 : 11 : 2 : 741 (1 specimen, alcohol).
Locality: Sta. 186. Fournier Bay, Anvers Island, Palmer Archipelago, Graham Land, 295 m, 16 March 1927.
Collection: " Discovery " Committee.

HAPLOOPS Liljeborg

Haploops securiger Barnard 1931 : 426.

Syntypes: Reg. no. 1936 : 11 : 2 : 742–746* (7 specimens, alcohol).
Locality: Sta. 123. Off entrance of Cumberland Bay, South Georgia, 230–250 m, 15 December 1926.

Syntypes: Reg. no. 1936 : 11 : 2 : 747–796 (17 + 6 + 4 + 2 + 21 + 21 + 6 + 1 specimens, alcohol).
Localities: Sta. 27. West Cumberland Bay, South Georgia, 110 m, 15 March 1926. Sta. 42. Off entrance of Cumberland Bay, South Georgia, 120–204 m, 1 April 1926. Sta. 140. Stromness Harbour to Larsen Point, South Georgia, 122–136 m, 23 December 1926. Sta. 144. Off entrance of Stromness Harbour, South Georgia, 155–178 m, 5 January 1927. Sta. 146. Off South Georgia, 53° 48′ S 35° 37′ W, 728 m, 8 January 1927. Sta. 153. Off South Georgia, 54° 08′ S 36° 27′ W, 106 m, 17 January 1927. Sta. 170. Off Cape Bowles, Clarence Island, South Shetland Islands, 61° 25′ S 53° 46′ W, 342 m, 23 February 1927. Sta. WS 33. Off South Georgia, 54° 59′ S 35° 24′ W, 130 m, 23 December 1926.

[***TETROMATUS*** Bate]

[*Tetromatus bellianus*] Bate 1856 : 58 (nom. nud.), 1857 : 139 (transferred to *Ampelisca brevicornis* (Costa) by Sars 1891).

Syntypes: Reg. no. 1952 : 5 : 7 : 27–29 (3 specimens, alcohol).
Locality: Moray Firth, Scotland.
Collection: Bate.

Family **HAUSTORIIDAE**

BATHYPOREIA Lindström

Bathyporeia elegans Watkin 1938 : 222 [*Bathyporeia pelagica* Sars 1891 : 129].

Syntypes: Reg. no. 1968 : 50 (2 specimens, alcohol).
Locality: Jaederen, Norway.
Collection: Zoological Museum, Oslo.

Bathyporeia pelagica (Bate) 1856 : 59 (nom. nud.), 1857 : 146 [*Theristes pelagica*].

HOLOTYPE: Reg. no. 1952 : 5 : 7 : 182 (alcohol).
LOCALITY: Moray Firth, Scotland.
COLLECTION: Bate.

[*Bathyporeia robertsoni*] Bate 1862 : 173 (transferred to *Bathyporeia pilosa* Lindström by Watkin 1938).

SYNTYPES: Reg. no. 1952 : 5 : 7 : 183–184 (2 specimens, alcohol).
LOCALITY: Cumbrae, Firth of Clyde, Scotland.
COLLECTION: Bate.

CARDENIO Stebbing

Cardenio paurodactylus Stebbing 1888 : 806.

SYNTYPES: Reg. no. 1889 : 5 : 15 : 58 (3 specimens in alcohol + 4 slides).
LOCALITY: Betsy Cove, Kerguelen, South Indian Ocean, surface, 10 January 1874.
COLLECTION: " Challenger ".

Also in the Museum Collection is the specimen on which Barnard (1932 : 91, fig. 43) based the description of the male of the species. He designated this specimen as " Type of ♂ " but in fact it has no type status.

HAUSTORIELLA Barnard

[*Haustoriella psammophila*] Barnard 1931 : 426 (transferred to *Phoxocephalopsis zimmeri* Schellenberg by Barnard 1932).

SYNTYPES: Reg. no. 1936 : 11 : 2 : 804–805 (2 specimens, alcohol).
LOCALITY: Sta. WS 96. NW of Falkland Islands, 48° 00′ S 64° 45′ W, 96 m, 17 April 1927.
COLLECTION: " Discovery " Committee.

PLATYISCHNOPUS Stebbing

Platyischnopus herdmani Walker 1904 : 247.

SYNTYPES: Reg. no. 1905 : 2 : 18 : 28–31 (4 specimens, alcohol).
1905 : 2 : 18 : 315–317 (3 slides).
1925 : 9 : 8 : 250–252 (2 specimens, alcohol).
LOCALITY: East Cheval Paar, Ceylon, November 1902.
COLLECTION: Herdman.

Platyischnopus mirabilis Stebbing 1888 : 830.

SYNTYPES: Reg. no. 1889 : 5 : 15 : 63 (4 slides).
LOCALITY: Port Jackson, Australia, 2–10 fm.
COLLECTION: " Challenger ".

PONTOPOREIA Krøyer

[*Pontoporeia hoyi*] Smith 1874 : 647 (transferred to *Pontoporeia affinis* Lindström by Gurjanova 1951).

SYNTYPES: Reg. no. 1911 : 11 : 8 : 13737–13746 (16 specimens, alcohol).
LOCALITY: Lake Superior, U.S.A., 50 fm, 1871.
COLLECTION: Norman.

UROTHOE Dana

Urothoe bairdi Bate 1862 : 114.

SYNTYPES: Reg. no. 1952 : 5 : 7 : 32–34 (6 specimens, alcohol).
LOCALITY: Moray Firth, Scotland.
COLLECTION: Bate.

Urothoe brevicornis Bate 1862 : 116.

SYNTYPES: Reg. no. 1952 : 5 : 7 : 35–37 (6 specimens, alcohol).
LOCALITY: Tenby, Wales.
COLLECTION: Bate.

Urothoe elegans (Bate) 1856 : 58 (nom. nud.), 1857 : 145 [*Gammarus elegans*].

SYNTYPE: Reg. no. 1952 : 5 : 7 : 139 (1 specimen, alcohol, badly mutilated).
LOCALITY: Plymouth, England.
COLLECTION: Bate.

Urothoe grimaldii Chevreux 1895 : 428.

SYNTYPES: Reg. no. 1911 : 11 : 8 : 14074–14077 (3 specimens, alcohol).
LOCALITY: Coast of Morocco.
COLLECTION: Norman.

Urothoe marina (Bate) 1857 : 140 [*Sulcator marinus*].

HOLOTYPE: Reg. no. 1952 : 5 : 7 : 141 (alcohol).
LOCALITY: Banff, Scotland.
COLLECTION: Bate.

Urothoe ruber Giles 1888 : 246.

SYNTYPES: Reg. no. 1968 : 54 (2 slides).
LOCALITY: Banks of the Chittagong River. The slide label gives the locality as Mutlah Flats.
COLLECTION: Giles.

Urothoe spinidigitus Walker 1904 : 245.

HOLOTYPE: Reg. no. 1905 : 2 : 18 : 26 (alcohol).
1905 : 2 : 18 : 314 (1 slide).
LOCALITY: Cheval Paar, Ceylon, November 1902.
COLLECTION: Herdman.

UROTHOIDES Stebbing

Urothoides lachneessa (Stebbing) 1888 : 825 [*Urothoe lachneessa*].

SYNTYPES: Reg. no. 1889 : 5 : 15 : 62 (part) (2 specimens, alcohol).
LOCALITY: Off Cumberland Bay, Kerguelen, South Indian Ocean, 120 fm.

SYNTYPES: Reg. no. 1889 : 5 : 15 : 62 (part) (6 slides).
LOCALITY: Off Christmas Harbour, Kerguelen, South Indian Ocean, 120 fm.
COLLECTION: " Challenger ".

The locality " off Christmas Harbour " is not mentioned by Stebbing (1888) under this species. It is probable, however, that this locality and " off Cumberland Bay " are the same, as the entrances of the two bays are only 9 km apart.

Urothoides oniscoides Barnard 1932 : 93.

HOLOTYPE: Reg. no. 1936 : 11 : 2 : 803 (alcohol).
LOCALITY: Sta. 196. Bransfield Strait, South Shetland Islands, 62° 17′ S 58° 21′ W 720 m, 3 April 1927.
COLLECTION: " Discovery " Committee.

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Square brackets enclosing only the generic name indicate species whose generic position has been changed since the original description of the species. Square brackets enclosing both the generic and specific names mark those species now considered to be junior synonyms. Round brackets indicate names of valid species which are not represented in the collections of the British Museum (Natural History) by type material, but which include type material of species now placed as junior synonyms.

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